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MEMORY AND PREDICTION IN SENTENCE PROCESSING

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MEMORY AND PREDICTION
IN SENTENCE PROCESSING

- EVIDENCE FROM BEHAVIORAL PERFORMANCE, EYE TRACKING, AND BRAIN IMAGING -

Von der Fakultät für Biowissenschaften, Pharmazie und Psychologie

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CONTENT

SUMMARY

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Memory and prediction in sentence processing

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Dissertation

Successful communication requires high-speed processing of current information, simultaneously linking the perceived information to our existing world knowledge, keeping in mind previous conversation contents and anticipating future input. The first part of the present thesis focuses on the memorization of linguistic input. Various researchers have pointed out that memorizing sentences differs substantially from memorizing unconnected words (cf. Baddeley, Hitch, & Allen, 2009; Brener, 1940; Jefferies, Ralph, & Baddeley, 2004; Potter & Lombardi, 1990, 1998; Rummer, 2003), demonstrating that humans are able to remember significantly more words correctly, if those words are presented within a sentence (i.e., the 'sentence superiority effect'; e.g. 'it is easier to recall many words in a sentence' vs. 'it sentence a in words many recall to easier is').

As the neurophysiological substrate of the beneficial effects of sentence structure on working memory remained to be examined, the first study of the present thesis investigated the brain mechanisms underlying the sentence superiority effect during encoding and during maintenance in a working memory task. A priori, sentence structure was assumed to lower the demands on the working memory system and, in consequence, to render rehearsal of sentences during the maintenance interval unnecessary. To test these hypotheses, all three aspects (i.e., sentence structure, working memory load, and rehearsal) were manipulated in one experiment.

On the behavioral level, ungrammatical word sequences led to decreased recall accuracy for high load items (six words) compared to low load items (four words); however, no such working memory load effect was evidenced for sentences fragments. The non-existence of a load effect in sentence fragments confirms that sentence structure reduces the demands on working memory capacity. In addition, remembering sentences correctly did not rely on the possibility to rehearse the items during working memory maintenance: Whereas the recall of ungrammatical word sequences was severely impaired in conditions that prevented item rehearsal during the maintenance phase, participants recalled sentence fragments equally well

in both conditions (i.e., with or without rehearsal). Thus, in line with previous literature, the present behavioral data suggest that memory processes fundamentally benefit from sentence structure.

In addition, the functional magnetic resonance imaging (fMRI) results depicted in chapter 0 allowed differentiating between the effects of sentence structure on the encoding and the maintenance of items in the working memory task. Encoding sentence fragments (as compared with the encoding of ungrammatical word sequences) recruited not only language-related areas such as inferior frontal (BA 47) and anterior temporal cortex that have previously been associated with semantic processing, but was also supported by the medial-temporal lobe (i.e. hippocampus/parahippocampus), a region typically reported for memory tasks. It should be stressed that the hippocampus was not sensitive to working memory load differences in the encoding phase, but rather to the availability of sentence structure. Medial temporal regions are not classically reported in linguistic tasks, but the interplay of language-specific and memory related brain systems is argued to mirror more elaborate encoding, potentially including chunking processes (i.e., binding single items into larger information units, thereby expanding working memory capacity, McNulty, 1966; Miller, 1956; Tulving & Patkau, 1962).

The increase of activity for sentence fragments during working memory encoding was followed by an activation *decrease* during maintenance in the prefrontal cortex and the inferior parietal sulcus. These regions are associated with attention and working memory, thus a reduced activity in these areas suggests load reduction effects of sentence structure during maintenance. A similar neurophysiological activation pattern of increased encoding and decreased maintenance activity has been reported by Bor and colleagues, who asked their participants to memorize structured versus unstructured items (e.g., 8 6 4 2 3 5 7 9 vs. a random sequence; cf. Bor, Cumming, Scott, & Owen, 2004a; Bor, Duncan, Wiseman, & Owen, 2003). Thus, structure seems to enrich encoding and alleviate maintenance both in linguistic and non-linguistic domains.

In addition, the maintenance phase revealed that maintaining items with a higher working memory load (six words) increased the engagement of Broca's area in comparison to low load items (four words) when participants memorized ungrammatical word sequences. However, no such working memory load effect was evidenced when participants memorized sentence fragments. Those results closely mirror the working memory load effects on the working memory performance of the participants in sentence fragments versus ungrammatical word sequences: Both performance and neuronal activity suggest a syntax-driven load reduction.

In summary, the sentence superiority effect is neurally reflected in a twofold pattern, consisting of increased activation in classical language and memory areas during the encoding phase (i.e., enriched encoding) followed by decreased maintenance-related activation, suggesting a less effortful sentence maintenance. This progression over the phases of the working memory process reflects how chunking during encoding (based on sentential syntactic and semantic information) alleviates maintenance demands and leads to improved working memory performance. Notably, the reduced activity during maintenance is speaking against the assumption that item maintenance is achieved via constant refreshment (and thus sustained activation) of the respective memory representations, as proposed by process models of working memory (Cowan, 1999; Zhou, Ardestani, & Fuster, 2007).

As mentioned in the beginning, successful communication not only relies on memorizing and keeping track of previous conversation contents. Instead, to speed up online processing, interlocutors are argued to utilize their memory contents (both preexisting knowledge stored in long-term memory and currently maintained working memory items) to anticipate future communication contents. The second part of the present thesis is thus dedicated to linguistic predictions, a processing mechanism that supposedly aids fast language comprehension. Predictive coding as a general principle of neurophysiological information processing (cf. de-Wit, Machilsen, & Putzeys, 2010; Friston & Kiebel, 2009; Rao & Ballard, 1999) has been suggested to improve sensory processing, relying on the assumption that our brain stores internal models of the world that lead to automatic anticipation of likely upcoming input (based on prior analogous experiences; cf. Bar, 2007, 2009). Given the rich language experience of an adult, and assuming that the concept of predictive coding translates to a higher-order cognitive process such as language, linguistic processing can be argued to comprise an anticipatory component with regard to different levels of linguistic processing (such as e.g. syntax, semantics, perceptual properties; cf. Dikker & Pylkkanen, 2011; Dikker, Rabagliati, Farmer, & Pylkkanen, 2010; Dikker, Rabagliati, & Pylkkanen, 2009; Federmeier, Wlotko, De Ochoa-Dewald, & Kutas, 2007; Lau, Stroud, Plesch, & Phillips, 2006; Levy, 2008; Pickering & Garrod, 2013; Smith & Levy, 2013).

However, experimental proof of the existence, timing, and underlying neural substrate of a linguistic prediction remains challenging. The present work introduces a new “predictive eye gaze reading task” that combines data from eye-tracking and human fMRI: Participants were presented with different types of word sequences (i.e., normal sentences, meaningless jabberwocky sentences, non-word lists), up to the pre-final target word. After a temporal delay of approximately five seconds, the final target word was displayed in a distinct screen position depending on the syntactic word category (e.g. nouns in the upper, verbs in the lower right corner). At this point, participants were asked to judge whether or not the final target word was a correct continuation of the preceding word sequence. Importantly, in order to find out whether or not participants would generate predictions automatically when linguistic input is delayed, participants were not instructed to predict the final target word.

Results from eye tracking indicated that participants indeed made anticipatory eye-movements into the correct target word region already *before* the target word was presented, thereby confirming the existence of linguistic predictions. Moreover, when the actual target word was presented after the prediction interval, participants were judging predicted target words faster and more accurately than unpredicted target words, providing evidence for behavioral benefits of predictive processes in language.

In order to extract the neurophysiological basis of linguistic predictions (in contrast to a non-word list control condition that did not provide a predictive context), in the fMRI analysis the timing of the prediction process was aligned to the timing of the anticipatory eye-movements. The fMRI results revealed that word category prediction was supported by a distributed network of cortical and subcortical brain regions, such as ventral premotor cortex, basal ganglia, thalamus, and hippocampus. These systems have been formerly associated with syntax and sequence processing (Fiebach & Schubotz, 2006; Lisman & Redish, 2009; Molinari et al., 2008; Price, 2010).

Besides these shared neural resources, pure word category prediction relied stronger on left-hemispheric language systems (such as left BA 44/45, anterior and posterior left superior temporal regions, dorsal caudate nucleus) than the prediction of a specific word. Word prediction in contrast was supported by rather right-lateralized cortical areas in the temporal and parietal cortices (associated with semantic processing) as well as occipital areas. Thus, the present results suggest a potential role for the right hemisphere in predictive language processes.

In sum, adults generate linguistic predictions during sentence comprehension without being instructed to – and these predictions are supported by language and sequence processing systems. These results are in line with a current model of language which proposes a fundamental role of predictions for communication (Pickering & Garrod, 2013). Moreover, the present findings suggest that predictions are not only an important aspect of natural verbal communication, but contribute to reading processes in the absence of an interlocutor as well.

Ultimately, as predictions are generated based on prior analogous experiences stored in memory, memory and prediction processes were hypothesized to draw on (partly) overlapping neural resources. An additional fMRI analysis was performed in order to test whether or not the results from both the memory and the prediction experiment can be integrated to reveal a shared neural substrate supporting both aspects of sentence processing. The results support the assumption of a common set of brain regions (i.e., angular gyrus, putamen, hippocampus, and cerebellum) for encoding words in a syntactic structure and predicting upcoming syntactic elements.

In conclusion, the experiments conducted for the present thesis provide strong evidence that both the successful memorization and predictive processes in the linguistic domain profit significantly from sentence structure. This benefit is observable across different measures such as behavioral performance and anticipatory eye movements. Neurophysiological reflections of enriched encoding and facilitated maintenance as well as the enhanced engagement of language and sequence processing brain regions during word category predictions provide additional evidence for the qualitative difference in information processing due to sentence structure. Moreover, a direct comparison between the brain systems in charge of encoding sentences into working memory versus predicting upcoming syntactic elements provides first evidence that the processes partly rely on shared neural resources. This result is in line with current theoretical proposals suggesting a tight connection between memory and prediction processes (Bar, 2007, 2009; Mullally & Maguire, 2014; Schacter, Addis, & Buckner, 2008) and extends the applicability of those approaches to the domain of language processing.

ZUSAMMENFASSUNG

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Erfolgreiches Kommunizieren erfordert eine schnelle und effiziente Sprachverarbeitung, was beinhaltet, dass einströmende Informationen mit Vorwissen in Verbindung gebracht werden, während simultan bisherige Kommunikationsinhalte behalten und zukünftiger Input antizipiert werden. Die vorliegende Arbeit behandelt die Frage, wie das menschliche Gehirn Satzstrukturen nutzt, um Gedächtnis- und Prädiktionsprozesse während der Satzverarbeitung zu optimieren.

Der erste Teil der Arbeit beschäftigt sich mit dem sogenannten „Satzüberlegenheitseffekt“. Das Phänomen „Satzüberlegenheit“ beinhaltet, dass Menschen in der Lage sind, sich eine sehr viel größere Anzahl an Wörtern zu merken, wenn diese in einer syntaktisch korrekten Reihenfolge dargeboten werden, als wenn die Reihenfolge ungrammatisch ist (z. B. „es ist leichter sich viele Wörter in einem Satz zu merken" versus „es viele sich einem merken ist Satz Wörter leichter in zu"; siehe Baddeley et al., 2009; Brener, 1940; Jefferies et al., 2004; Potter & Lombardi, 1990, 1998; Rummer, 2003). In den Studien, die im Rahmen der vorliegenden Arbeit durchgeführt wurden, konnte bestätigt werden, dass das Vorhandensein einer Satzstruktur den Probanden tatsächlich hilft, größere Mengen an Wortmaterial im Arbeitsgedächtnis zu behalten: Während sechs Wörter in ungrammatischer Reihenfolge zu einer schlechteren Erinnerungsleistung führten als vier Wörter, konnte kein derartiger Performanzabfall zwischen vier und sechs Wörter gefunden werden, wenn diese in einer Satzstruktur dargeboten wurden. Zudem wurde gezeigt, dass der positive Einfluss einer Satzstruktur unabhängig davon ist, ob die Probanden während der sogenannten Behaltensphase (also der Phase zwischen Erlernen (Enkodieren) und Wiedergabe (Abruf)) das Material innerlich wiederholen konnten: Probanden gaben die Satzfragmente mit oder ohne stille Repetitionen vergleichbar gut wieder, während sie in ungrammatischen Wortsequenzen schlechtere Gedächtnisleistungen erbrachten, wenn sie das Material nicht wiederholen konnten.

Um die neurophysiologische Grundlage dieser Effekte zu identifizieren, wurden parallel zur Ausführung der Arbeitsgedächtnisaufgabe funktionelle Magnetresonanz-Tomographiedaten

erhoben. Der direkte Vergleich von Satzfragmenten und ungrammatischen Wortsequenzen in der Enkodierungs- und der Aufrechterhaltungsphase legt eine Reihe von Schlüssen nahe, die in den kommenden Absätzen kurz zusammengefasst werden.

Bei der Enkodierung von Sätzen wurde Hirnareale aktiviert, die gemeinhin mit semantischer Verarbeitung (z. B. der inferiore Gyrus frontalis und der anteriore Teil des Gyrus temporalis medius) und Gedächtnisprozessen (Hippocampus/Parahippocampus) assoziiert werden. Hippocampus und Parahippocampus werden in klassischen Sprachstudien nur selten gefunden, ihre Beteiligung wird als Anzeichen für einen Chunking-Prozess interpretiert, also ein Zusammenfassen („chunking") von Einzelelementen in größere, bedeutungsvolle Gedächtnisrepräsentationen (vgl. McNulty, 1966; Miller, 1956; Tulving & Patkau, 1962). Dass Chunking bei Satzfragmenten Anwendung finden und somit zu einer – im Vergleich zu ungrammatischen Wortsequenzen – verbesserten Enkodierung führen könnte, scheint plausibel: Ein Satz(-Fragment) enthält im Vergleich zu einzelnen unrelatierten Wörter eine zusätzliche, übergeordnete Bedeutung, die ermöglicht, dass der Satz als gesamte Bedeutungseinheit („chunk") gespeichert werden kann (anstelle einer separaten Speicherung aller einzelner Wörter).

In der Behaltensphase hingegen verursachten die Satzfragmente ein geringeres Aktivitätsniveau als die ungrammatischen Wortsequenzen in Arealen, die in der Literatur mit Arbeitsgedächtnis und Aufmerksamkeit assoziiert werden (z.B. präfrontal Areale, das supplementärmotorische Areal und parietale Regionen). Bemerkenswerterweise spiegelt sich die Erinnerungsperformanz für Satzfragmente und ungrammatische Wortfolgen in der Aktivität des Broca-Areals (Brodmann-Areal 44/45) wider: Während längere Satzfragmente (im Vergleich zu kürzeren) keinen Anstieg der neurophysiologischen Aktivität im Broca-Areal verursachten, reagierte das Broca-Areal mit stärkerer Aktivierung auf längere ungrammatische Wortsequenzen.

Zusammenfassend lässt sich sagen, dass das Erinnern von Satzfragmenten durch stärkere neurophysiologische Aktivierung während der Enkodierungsphase und ein reduziertes Aktivitätslevel in der Aufrechterhaltungsphase gekennzeichnet ist – ein Muster, dass bereits in einer Studie von Bor und Kollegen für Erinnerungsprozesse bei strukturierten vs. unstrukturierten Sequenzen berichtet wurde (z.B. 8 6 4 2 3 5 7 9 versus eine zufällige Sequenz; siehe Bor et al., 2004a; Bor et al., 2003). In der vorliegenden Arbeit wird argumentiert, dass dieses Muster eine umfangreichere Enkodierung widerspiegelt, die eine weniger aufwendige und weniger auf stille Repetitionen angewiesene Behaltensphase zur Folge hat, was sich wiederum in einem reduzierten neuronalen Aktivitätsniveau ausdrückt. Allerdings steht das hier gefundene Aktivierungsmuster (gesteigert während der Enkodierung, reduziert in der Behaltensphase) im Gegensatz zu Annahmen der Prozessmodelle des Arbeitsgedächtnisses, die Behaltensleistungen auf fortwährend aufgefrischte Aktivierung der entsprechenden Repräsentationen im Gehirn zurückführen (Cowan, 1999; Zhou et al., 2007).

Wie zu Beginn angemerkt, könnte die Satzstruktur nicht nur beim Erinnern, sondern auch bei der Prädiktion möglicher zukünftiger linguistischer Elemente eine tragende Rolle spielen. Prädiktive Prozesse werden seit einiger Zeit als wichtiger Bestandteil der generellen Informationsverarbeitung angesehen (vgl. de-Wit et al., 2010; Friston & Kiebel, 2009; Rao & Ballard, 1999). Es wird argumentiert, dass die aktuell wahrgenommenen Informationen nicht nur im Gedächtnis gespeichert werden, sondern auch die Aktivierung bereits gespeicherter ähnlicher Repräsentationen anregen, die dann wiederum helfen können vorherzusagen, was wahrscheinlich als nächstes passieren wird. Diese Vorhersage wird anschließend mit dem tatsächlichen Input abgeglichen, und nur dann, wenn eine Differenz zwischen Vorhersage und Input besteht, muss die tatsächliche Information überhaupt von den sensorischen Hirnarealen in diejenigen Hirnareale transferiert werden, die für höhere kognitive Leistungen zuständig sind und die internen Modelle der Welt, die für die Vorhersagen zuständig sind, überarbeiten. Auf diesem Wege kann der Informationstransfer bottom-up bedeutend reduziert und die Verarbeitungsgeschwindigkeit erhöht werden. In der Annahme, dass sich dieses allgemeine Verarbeitungsprinzip auch auf komplexere kognitive Funktionen wie Sprache anwenden lässt, und unter Berücksichtigung der großen Erfahrung, die Erwachsene mit Sprachverarbeitung haben, wird angenommen, dass auch in der Sprachverarbeitung Vorhersagen bezüglich verschiedener Aspekte (z. B. Syntax, Semantik, perzeptuelle Eigenschaften) getroffen werden (vgl. Dikker & Pylkkanen, 2011; Dikker et al., 2010; Dikker et al., 2009; Federmeier et al., 2007; Lau et al., 2006; Levy, 2008; Pickering & Garrod, 2013; Smith & Levy, 2013).

Allerdings ist der experimentelle Nachweis der Existenz, des Zeitpunktes und der zugrundeliegenden Hirnprozesse von linguistischen Vorhersagen alles andere als trivial. Die vorliegende Arbeit stellt eine neue experimentelle Herangehensweise vor („predictive eye-gaze reading task“), die es ermöglicht, Eye-Tracking- und fMRT-Daten miteinander zu kombinieren, um Prädiktionen auf die Spur zu kommen. Den Probanden wurden verschiedene Arten von Wortsequenzen dargeboten (normale Sätze; bedeutungslose, aber grammatikalisch korrekte Jabberwocky-Sätze; Nicht-Wort-Listen), und zwar bis zum vorletzten Wort. Nach einer Verzögerung von einigen Sekunden wurde das letzte (Ziel-)Wort präsentiert, je nach Wortkategorie (Nomen vs. Verb) an einer spezifischen Bildschirmposition. Während der Präsentation mussten die Probanden entscheiden, ob das Zielwort eine grammatikalisch korrekte Weiterführung der vorherigen Wortsequenz darstellt. Es sei angemerkt, dass die Probanden nicht durch Instruktion dazu aufgefordert wurden, Vorhersagen bezüglich des Zielwortes zu treffen, denn es sollte herausgefunden werden, ob sie Vorhersagen automatisch treffen.

Tatsächlich konnte in den Eye-Tracking-Daten festgestellt werden, dass die Probanden ihre Augen antizipatorisch auf diejenige Bildschirmregion richteten, in der das grammatikalisch korrekte Zielwort auftauchen würde; darüber hinaus zeigte die behaviorale Performanz eindeutig, dass die Entscheidung, ob das Zielwort passend oder unpassend ist, schneller getroffen wurde, wenn das vorhersagbare Zielwort gezeigt wurde. Hiermit wurde einerseits der Nachweis für einen stattfindenden prädiktiven Prozess erbracht und auf der anderen Seite auch der Performanz-Vorteil von Vorhersagen demonstriert: Vorhergesagte Wörter werden schneller verarbeitet.

Um die Hirnprozesse zu identifizieren, die den sprachlichen Prädiktionen zugrundeliegenden, wurde ein fMRT-Experiment durchgeführt, in dessen Analyse der Zeitpunkt der Prädiktion des Probanden anhand der antizipatorischen Augenbewegung bestimmt wurde. Die Ergebnisse zeigen, dass innerhalb von normalen und Jabberwocky-Sätzen die Vorhersage einer Wortkategorie wie „Verb“ oder „Nomen“ durch Aktivierung eines weitverteilten Netzwerkes aus kortikalen und subkortikalen Hirnarealen (z. B. der ventrale prämotorische Kortex, die Basalganglien, den Thalamus und Hippocampus) gestützt wird – Areale, die mit der Verarbeitung von Syntax und Sequenzen in Verbindung gebracht werden (Fiebach & Schubotz, 2006; Lisman & Redish, 2009; Molinari et al., 2008; Price, 2010).

Zusätzlich zu den Hirnarealen, die sowohl an der Vorhersage von Wortkategorien und spezifischen Wörtern beteiligt waren, führt eine ausschließliche Vorhersage von Wortkategorien (im Kontext von bedeutungslosen Jabberwocky-Sätzen) zu einer Aktivierung von linkshemisphärischen Sprachsystemen (Broca-Areal, anteriore und posteriore Anteile des Gyrus temporalis superioris, Nucleus caudatus dorsalis). Dagegen ist die Vorhersage eines spezifischen Wortes in normalen Sätzen durch Aktivierung von Arealen vorwiegend in der rechten Hemisphäre gekennzeichnet; insbesondere temporale und parietale Regionen (assoziiert mit semantischer Verarbeitung) und der Okzipitallappen (visuelle Verarbeitung) sind hierbei zu nennen. Die Ergebnisse der vorliegenden Arbeit legen daher eine mögliche Rolle rechtshemisphärischer Areale für sprachliche Vorhersagen nahe.

Zusammengefasst lassen die Ergebnisse der hier vorgestellten Prädiktionsstudie darauf schließen, dass Erwachsene während der Satzverarbeitung zukünftige linguistische Elemente antizipieren (ohne, dass sie dazu instruiert werden müssen) und dass linguistische Vorhersagen durch Aktivierung von Hirnarealen ermöglicht werden, die mit Sprach- und allgemeiner Sequenzverarbeitung in Verbindung stehen. Diese Ergebnisse stehen in Einklang mit einem neuen Sprachmodell von Pickering and Garrod (2013), welches prädiktiven Prozessen eine wichtige Rolle in der Kommunikation einräumt, und deuten ferner darauf hin, dass Prädiktionen nicht nur für direkte mündliche Kommunikationssituationen, sondern auch für Leseprozesse hilfreich sind.

Da Vorhersagen nur auf Basis im Gedächtnis gespeicherter vorheriger Erfahrungen getroffen werden können, wird im dritten Teil der vorliegenden Arbeit untersucht, ob Prädiktions- und Gedächtnisprozesse (teilweise) auf gemeinsame neuronale Ressourcen zurückgreifen. Um diese Frage zu beantworten, wurden die fMRT-Daten aus der Enkodierungsphase der Arbeitsgedächtnisstudie und der Vorhersagephase der Prädiktionsstudie gemeinsam analysiert. Die Ergebnisse dieser Analyse bestätigen die Annahme eines gemeinsamen neuronalen Netzwerks aus Gyrus angulares, Hippocampus, Thalamus und Putamen für die Speicherung von Satzfragmenten *und* die Vorhersage der Wortkategorie des nächsten Wortes.

Die im Rahmen der vorliegenden Arbeit durchgeführten Studien erlauben daher folgende Schlussfolgerungen: Sowohl der Erinnerungsprozess als auch linguistische Vorhersagen profitieren deutlich von der Verfügbarkeit einer Satzstruktur. Dieser Nutzen offenbart sich in unterschiedlichen Bereichen, sowohl in der behavioralen Performanz (Erinnerungsleistungen und Grammatikalitätsbeurteilungen), als auch in antizipativen Augenbewegungen und im zugrundeliegenden neuronalen Aktivitätsmuster: Eine verbesserte Enkodierung und vereinfachte Aufrechterhaltung von Satzfragmenten im Gedächtnis – verglichen mit ungrammatikalischen Wortsequenzen – spiegelt die positiven Effekte einer Satzstruktur ebenso wider wie die Aktivität von Sprach- und Sequenzverarbeitungsregionen während einer linguistischen Prädiktion. Darüber hinaus scheinen Gedächtnis- und Prädiktionsprozesse von einem ähnlichen Netzwerk von Hirnarealen ermöglicht zu werden. Dieses Ergebnis stützt neuere theoretische Überlegungen, die eine starke Interdependenz dieser Prozesse postulieren (Bar, 2007, 2009; Mullally & Maguire, 2014; Schacter et al., 2008), und legt nahe, dass sich diese allgemeinen Konzepte vom Zusammenhang zwischen Gedächtnis und Prädiktion auf die Sprache übertragen lassen.

1 GENERAL INTRODUCTION

Imagine you are sitting in a café with your best friend, discussing what concerns you the most. At the moment, your friend is talking about private matters. Now freeze the scenario in your imagination before your friend has finished the sentence - and spend some thought on the cognitive prerequisites and ongoing processes that are essential to render this conversation possible.

Starting with the cognitive prerequisites, you need an efficient memory system that provides you with all the background knowledge essential to understand what is communicated. Although you are not constantly consciously aware of it, your brain stores a large body of linguistic knowledge regarding the meaning of words, the syntactic rules of language that allow yout to combine single words into a sentence level meaning (Berwick, Friederici, Chomsky, & Bolhuis, 2013; Binder, Desai, Graves, & Conant, 2009; Chomsky, 1956; Frazier, 1987; Friederici, 2011; Petersson & Hagoort, 2012) and even more, to a cumulative meaning of longer text passages or conversations with multiple speakers. It also includes world knowledge regarding the topic your friend is discussing with you, information you collected during previous conversations with your friend regarding his private life, his way of thinking about certain subjects, his attitude towards certain topics, et cetera. Possessing a memory system that stores all of this background knowledge establishes a solid basis for understanding the information your friend passes on to you. This knowledge has to be activated and used during the conversation.

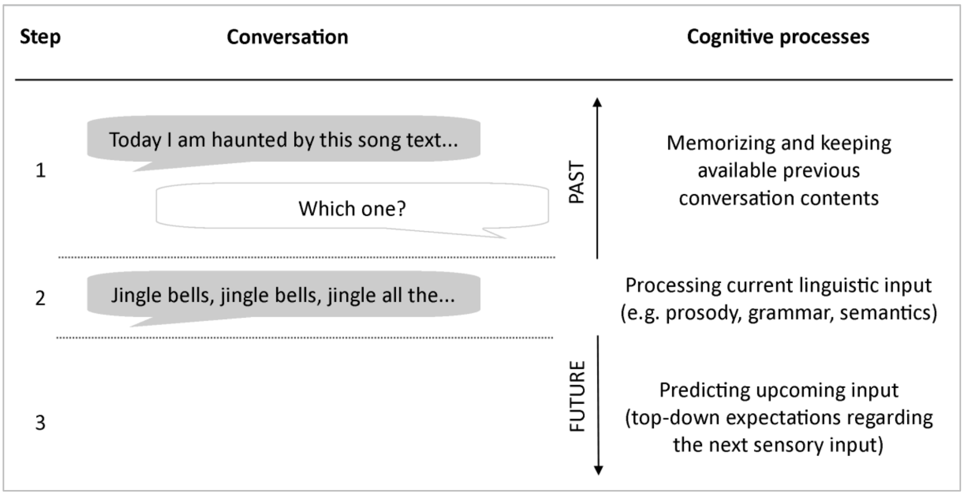

Figure 1-1: Schematic depiction of concurrent cognitive processes during a conversation.

Think about the conversation on a time line (as illustrated in Figure 1-1). Your friend is about to finish the sentence. On the one hand, you need to be able to store the conversation contents over the course of not only one, but maybe several sentences, to have in mind what your friend has said so far, and what you replied (Figure 1-1, step 1). This information might not enter your long-term knowledge yet; when asked about it in a couple of weeks, you probably will not remember all the details. But during the conversation, you bear in mind the meaning of what is said, in order to be able to think about the information and prepare your response. Humans perform extraordinarily well when asked to recall sentences they have been presented with; they are able to reproduce more than twice as many word correctly in sentences compared to recalling word lists (Brener, 1940). The first part of the present thesis is focused on sentence maintenance over short time periods, investigating how sentence structure improves memory performance and identifying the neural substrate of sentence encoding and maintenance (see chapter 0).

However, to be able to memorize previous conversation contents, the information has to be processed in the first place (cf. Figure 1-1, step 2), using all available information, be it semantic, syntactic, prosodic, et cetera (for comprehensive reviews the interested reader is pointed to Binder et al., 2009; Friederici, 2011; Hagoort, 2005a). A large body of research investigated how those processes are trained over ontogenesis across different languages and cultures, demonstrating how early in life we develop the ability to extract single words from continuous word streams, learn their meaning, and are able to understand the accumulated meaning of word sequences (see e.g. Friederici, 2005; Kuhl, 2004). Possessing a language system that has been trained over many years, we process linguistic contents automatically and seemingly effortlessly. However, as the rate of input during conversations is very high and we are expected to prepare our responses while our vis-à-vis is still talking, efficiency of language processing might be improved by a top-down mechanism: the prediction of the next sensory input (Figure 1-1, step 3).

It has been proposed recently that the brain in general not only holds capacities to parse and store information, but also links the current input to existing knowledge, thereby simultaneously generating top-down expectations regarding the probable next events (Friston & Kiebel, 2009; Rao & Ballard, 1999; Sohoglu, Peelle, Carlyon, & Davis, 2012). Moshe Bar even argued that one important benefit of the human ability to remember is to be able to anticipate future events in similar situations by means of analogy building (Bar, 2009). Following this logic, additionally to comprehending the ongoing conversation, we might be able to anticipate what is coming next. The investigation of the specific prediction of future linguistic input and its underlying neural processes constitute the second major focus of the present thesis and will be detailed in chapter 4.

To sum up, the research performed over the course of the present thesis spotlights two aspects out of the multitude of ongoing cognitive processes that are essential for a conversation: Memorizing and predicting linguistic input. Before concentrating on the nature of predictions regarding *future* linguistic events, the following section will begin with introducing the general theoretical background regarding the memorization of *past* linguistic information. After characterizing working memory processes for words bound in sentence structure, all behavioral and neurophysiological hypotheses regarding the beneficial effects of sentence structure on memory performance are detailed in the following section.

1.1 MEMORIZING WORDS

Memorizing linguistic contents in a sentence context seems to differ considerably from storing other types of items in memory (Brener, 1940; Jefferies et al., 2004; Perham, Marsh, & Jones, 2009; Potter & Lombardi, 1990; Rummer, 2003). Brener (1940) demonstrated that participants are able to memorize a larger number of words if those words are ordered in a grammatically acceptable way (compared to unrelated words in a word list). This result also applies to the comparison of grammatical versus ungrammatical word sequences; for example, a sequence such as

> *"words in a grammatical order are easier to remember"*

is easier to process and remember than

> *"words easier a remember to order in grammatical are"*,

although both sequences contain the exact same words. This so called "sentence superiority effect" has been replicated even with short sentences fragments down to two-word combinations (Jefferies et al., 2004; Perham et al., 2009). In other words, on the behavioral level a reduction in working memory load due to sentence structure has been observed. One might argue that this load reduction in turn leads to a reduced necessity to rehearse sentences (as compared to word lists) during the retention phase. Both aspects (i.e. the effect of sentence structure on working memory load and its influence on rehearsal) will be investigated in the present study, including the examination of their neural substrate. The following two sections will provide a theoretical background on potential effects of sentence structure and highlight the hypotheses for the working memory study depicted in chapter 0.

1.1.1 INFLUENCES OF SENTENCE STRUCTURE ON THE STAGES OF MEMORIZING AND MEMORY CAPACITIES

While there is an agreement about the facilitative effects of sentence structure on memory in general, the question remains how the sentence structure influences the consecutive stages of the memory process: the encoding, maintenance, and recall of information (cf. Chein & Fiez, 2001). Which characteristics of sentence structure might alleviate memorizing words? In general, sentence structure specifies the relation of words on a semantic level, and it offers a rule system for sequencing words. The conceptual regeneration hypothesis states that in case of sentences, both the semantics and the syntactic structure are primed from encoding to recall (Potter & Lombardi, 1990, 1998), thereby alleviating the recall of sentences; in contrast, word lists are proposed to be remembered mainly based on the phonological information. In line with this, a special recall process for sentences is proposed by Rummer and colleagues as well (cf. Engelkamp & Rummer, 1999; Rummer, 2003). The authors point out that sentence structure might be especially useful because a sentence has to be re-generated at recall utilizing the latest activated items in memory; this re-generation is thought to be a production process, which is easily accomplished in a grammatically "allowed" word order, because this is the standard way of sequencing words which has to be actively suppressed when producing ungrammatical word sequences. However, behavioral experiments regarding memory performance usually measure response times and accuracy of responses at recall. Relying exclusively on behavioral paradigms thus makes it difficult to dismantle the influences of sentence structure during earlier stages of the memory process, namely encoding and maintenance of information. For this reason, one major objective of the present thesis was to investigate the effects of sentence structure during encoding and maintenance by means of neurophysiological measures.

In summary, the present study was designed to (a) replicate the sentence superiority effect in terms of behavioral performance, (b) extract its neural substrate, and to (c) investigate its influences on working memory load and rehearsal strategies on both behavioral and neurophysiological levels. In order to cover all aspects in one experimental design, six conditions were generated, including trials with and without sentence structure, with high and low working memory load, and trials in which rehearsing the memoranda during maintenance was allowed or prevented[1]. As one part of the research question comprised disentangling the different stages of the memorizing process at the neurophysiological level, the sentence superiority effect was assessed via functional magnet resonance imaging (fMRI), which permits tracking the brain responses over the course of the memorizing process.

Prior to fMRI measurements, a new stimulus set had to be created to comply with all requirements set by the conditions detailed above. Both the creation of the stimulus set as well as the behavioral pilot study are described in the method section 2.4.1; the subsequent fMRI study has been published in the Journal of Cognitive Neuroscience (Bonhage, Fiebach, Bahlmann, & Mueller, 2014; see chapter 3).

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[1] Rehearsal refers to a silent repetition of the items one has to remember and can be effectively reduced by asking the participants to utter unrelated speech during the retention interval, which reduces memory performance (i.e., Articulatory Suppression; cf. Baddeley et al., 2009; Hanley & Thomas, 1984; Murray, Rowan, & Smith, 1988)

1.1.2 HYPOTHESES

The hypotheses section is split into two parts: The effects regarding (a) behavioral performance and (b) the neurophysiological responses induced by the experimental conditions. Starting with the behavioral performance, the following results were expected:

1. Higher performance (i.e., faster response times and increased accuracy) for stimuli with than without sentence structure.
2. Higher performance for shorter than longer word sequences (i.e., working memory load effect).
3. Higher performance in trials that allow rehearsal of items during maintenance than in trials with Articulatory Suppression.
4. A reduction of the load and the Articulatory suppression effect in the presence of sentence structure.

In order to generate hypotheses regarding the neural substrate of the sentence superiority effect during encoding and maintenance of information, it is necessary to put the phenomenon into the context of existing neurophysiological models of working memory. Before introducing the models and their neural premises, remember that sentence structure specifies both the sequential order and the associative/semantic relations of words. Although it is beyond question that ungrammatical word sequences in the present experiment do not meet the syntactic expectations regarding the sequential order of words, it might be argued that they still contain the same information as sentences on a lexico-semantic level. Establishing semantic relations between semantic contents during encoding thus should be possible in ungrammatical word sequences; yet without the backbone of intact sentence structure the information is far less specific and reliable. Therefore, two additional sorts of information are available when encoding sentences instead of word lists: the sequential and the semantic relations between words.

In the context of the active memory model (Zhao et al., 2007) or the embedded processing model of working memory by Cowan (Cowan, 1999), (verbal) working memory is thought to be reflected in sustained (i.e., periodically updated) activation of currently relevant language representations in long term memory, including all properties of linguistic information (e.g. semantics, syntax, phonology). This conception is supported by studies demonstrating that both word-level semantic (Fiebach, Friederici, Smith, & Swinney, 2007) and lexical information (Fiebach, Rissman, & D'Esposito, 2006) improve working memory performance; this effect was accompanied by engagement of language-related brain systems during maintenance.

Another theoretical approach to working memory that may contribute to the understanding of the sentence superiority effect was proposed by Cohen, Poldrack, and Eichenbaum (Cohen, Poldrack, & Eichenbaum, 1997; Cohen et al., 1999; Konkel & Cohen, 2009; Konkel, Warren, Duff, Tranel, & Cohen, 2008), who suggest a "relational memory": the authors argue that not only single elements are encoded (i.e., item memory), but their interrelation is stored as well (i.e., relational memory). Although Cohen and colleagues do not make claims regarding linguistic memory contents, their model seems capable of capturing the information provided by sentence structure quite nicely – both the associative-semantic and sequential relation of words could potentially be stored in a relational memory system. Linking the concept of relational memory to neurophysiology, Konkel and Cohen (2009; 2008) suggest that the encoding of various types of relations (e.g., spatial, sequential, and associative) into memory is supported by the hippocampus; consequently, it is here hypothesized that the hippocampus may play a role in the encoding of sentences.

A further conception of the working memory system, the so-called multiple component model also provides a framework for understanding the sentence superiority effect. The model (Baddeley, 2000, 2010; Baddeley et al., 2009; Baddeley & Logie, 1999) consists of four components: A visual and a phonological short-term buffer which store the latest input of the respective domain; an episodic buffer that interfaces and integrates short-term and long term memory contents, and an attentional system with a limited capacity, the so-called central executive. Investigating the controlled integrative encoding of sentences, Jefferies and Baddeley (2004) suggest that sentence structure triggers chunking of single elements into larger meaningful units that can be recalled later more effortless. Chunking has been regarded one of the most powerful ways to expand working memory capacities for a long time (e.g. McNulty, 1966; Miller, 1956; Tulving & Patkau, 1962); humans are assumed to be able to memorize a specific number of chunks rather than elements.

Initially, Jefferies and Baddeley pinned the item-binding chunking process down to the domain of executive control functions, which have been supposed to rely on engagement of the frontal and parietal lobes (for a review, see Collette & Van der Linden, 2002; D'Esposito et al., 1995) rather than medial temporal regions. This assumption would be in line with findings from Bor and colleagues, who found that the lateral prefrontal cortex shows increased activity when structured (versus unstructured) number sequences are encoded into working memory (e.g., 8 6 4 2 3 5 7 9 vs. a random sequence; cf. Bor et al., 2004a; Bor et al., 2003). However, in a later systematic investigation of the sentence superiority effect, Baddeley, Hitch and Allan (2009) reported its independence from attention-demanding concurrent tasks (e.g. visuo-spatial tasks). A priori they assumed that these concurrent tasks depend on the same limited resource (i.e., executive control) and thus should diminish the sentence superiority effect. However, as the results demonstrated that the sentence superiority effect was not influenced by the concurrent tasks, the authors concluded that chunking in sentences is an automatic rather than controlled encoding process that relies on the episodic buffer rather than the central executive. If this assumption holds true, the encoding of sentences should be mirrored in increased activity of those brain regions underlying the episodic buffer, such as the hippocampus (Berlingeri et al., 2008; Luck et al., 2010; M. Rudner & J. Ronnberg, 2008) or the lateral parietal cortex (von Allmen, Wurmitzer, Martin, & Klaver, 2011).

During maintenance, Bor and colleagues reported a reduction of neuronal activity for the abovementioned structured item sequences (e.g. 8 6 4 2 …) compared to the maintenance of unstructured sequences (Bor et al., 2004a; Bor et al., 2003). In line with these results, in the present study it was hypothesized that presenting words in a grammatical (i.e., structured) order also reduces neuronal activity: Sentence structure supposedly reduces the load on working memory capacities, which in turn potentially renders memory strategies such as rehearsal unnecessary. Therefore, improved encoding of sentences is hypothesized to result in an alleviated maintenance of information, leading to decreases of neurophysiological activation compared to the maintenance of ungrammatical word sequences. More specifically, the temporary maintenance and manipulation of currently relevant information (Curtis & D'Esposito, 2003; Rottschy et al., 2012; Salmon et al., 1996) as well as working memory load increases have been reported to result in activation increases in a fronto-parietal network (cf. Cowan et al., 2011; Jensen & Tesche, 2002; Manoach et al., 1996; Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999). If sentence structure reduces load, then the load-related neurophysiological activation should be decreased in items providing sentence structure (which is in line with the reduced maintenance demands proposed by Bor et al., 2003).

Turning to the second aspect of the former hypothesis, the reduced rehearsal demands for sentences, it is crucial to provide a definition of rehearsal: If the improved encoding of sentences reduces the necessity to use a memory strategy like rehearsal during maintenance, then activity in regions associated with rehearsal (such as left prefrontal cortex, bilateral SMA, parietal, and cerebellar cortices; cf. S. H. A. Chen & Desmond, 2005; Davachi, Maril, & Wagner, 2001; Logie, Venneri, Della Sala, Redpath, & Marshall, 2003) is hypothesized to decrease in items providing sentence structure.

In summary, the syntactic prediction fMRI study in chapter 0 tests the following neurophysiological hypotheses:

1. The encoding of sentences (as compared to the encoding of ungrammatical word sequences) involves areas responsible for the processing of syntax and associative/semantic contents as well as brain systems supporting sequence processing.
2. Being asked to remember a greater number of words (i.e., higher working memory load; 6 vs. 4 words) results in a stronger demands on brain systems that support working memory maintenance, as indicated by more neuronal activity in the respective regions.
3. However, these increased working memory demands due to a larger set of memoranda are reduced, if the task is to remember a sentence instead of an ungrammatical word sequence (interaction: sentence structure x working memory load).
4. Similarly, sentence structure might lead to decreased demands on the brain regions implicated in rehearsal compared to unstructured items (interaction: sentence structure x Articulatory Suppression).
5. Overall, maintaining sentences in working memory should trigger less neuronal activity than maintaining ungrammatical word sequences.

However, as mentioned in the first part of the introduction, beneficial effects of sentence structure are not only hypothesized for memorizing *past* information, but are expected to expand into *future* language processing as well. Indeed, the current linguistic input might not only be stored in working memory, but also trigger the activation of knowledge pre-existing in long term memory, which enables the language system to generate predictions about upcoming input. Therefore, the next section will focus on the anticipation of future linguistic information, introducing theoretical considerations and research regarding predictive processes in language.

1.2 PREDICTING WORDS

"To predict or not to predict: That is the "[2]

Reading the line above, you probably recognized that the sentence final word is missing – and that it should be "question". You might have experienced a similar phenomenon when someone is struggling to find the right word and you assist with what you assume to be the missing piece. Moreover, sometimes people cut in while someone else is speaking, not waiting for him to finish his thought. Why do we interrupt? Why do we complete unfinished sentences? Most likely because we assume we know where the sentences take us. Independent of whether we are ultimately right or wrong, we automatically generate predictions about upcoming input. However, why would the brain engage in an additional resource-consuming process such as prediction instead of waiting until the entire information is provided?

1.2.1 BENEFITS OF PREDICTIVE PROCESSING FOR EFFICIENT INFORMATION PROCESSING

Linguistic communication requires perceiving and understanding vast amounts of information within brief time intervals, thus it is inevitable to handle the input in an efficient way. One way towards fast and efficient information handling is to use the information available in working memory and knowledge stored in long term memory to proactively predict upcoming input. Predictive processing has been argued to be one fundamental principle of brain function (Friston & Kiebel, 2009; Huang & Rao, 2011; Rao & Ballard, 1999): Proponents of the predictive coding model argue that the brain generates hypotheses about the external world based on previous experiences; these hypotheses being predictions regarding upcoming sensory events. One of the potential advantages of sensory predictions is that the actual sensory input only has to be communicated in a bottom-up fashion (i.e., from sensory cortices to higher-level cognitive systems such as the prefrontal cortex) if the predictions are erroneous. Such a "prediction error" (i.e., a mismatch between the anticipated and the actual sensory input) would be communicated to brain areas that store or generate internal models of the world, forcing an adjustment of the internal model according to the unexpected input. However, a large proportion of the sensory information at any given time is not surprising, as it is quite similar to the preceding input or very expectable based on prior experiences. Therefore, instead of transmitting all sensory information to higher-order cognitive cortices, the amount of bottom-up information transfer can be reduced dramatically if only new or unexpected

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[2] Adapted from the famous quote by Hamlet "To be or not to be: That is the question" (William Shakespeare, 1603).

sensory input is conveyed. In sum, maximizing the efficiency of perception is thought to be achieved by minimizing propagation of redundant or predictable information.

1.2.1.1 PREDICTIVE PROCESSES IN THE HIGHER-LEVEL COGNITIVE DOMAIN OF LANGUAGE

In recent years it is assumed that predictive processing is integral part of higher-level cognitive functions such as language (cf. Arnal & Giraud, 2012; Dikker & Pylkkanen, 2011; Dikker et al., 2010; Dikker et al., 2009; Jakuszeit, Kotz, & Hasting, 2013; Pickering & Garrod, 2013; Sohoglu et al., 2012). In the specific case of language, such a prediction would rely on a combination of structural aspects of language (i.e., the grammatical rules, syntax) and the sentence context (i.e. sentence level meaning, semantics). The simple basic assumption is that on the one hand, the context has to be constraining in order to trigger a prediction; additionally, the more linguistic cues are available, the more reliable the prediction. In line with this simple proposal, a recent psycholinguistic theory by Levy suggests that the more constraining context becomes available to the recipient (e.g. over the course of a sentence), the less "surprised" the recipient is about the specific next word (Levy, 2008; Smith & Levy, 2013). Please note that "surprise" in this case is conceptually equivalent to "prediction error" (Schwartenbeck, Fitzgerald, Dolan, & Friston, 2013), linking this current psycholinguistic model to fundamental neuroscientific theories. However, as inspiring the idea of predictive processes in language might be, investigating predictions bears some serious experimental challenges.

1.2.1.2 METHODOLOGICAL CONSIDERATIONS IN PREDICTION RESEARCH

As predictive processes in language enjoy increasing attention (for a comprehensive review, see Pickering & Garrod, 2013), neuroscientists are facing one major pitfall: Directly proving the existence of a prediction and assessing its time stamp remains an experimental challenge, because typically predictions are not directly assessable to observation. Most of the previous research in humans relies on backward inferences (participants were faster to process later stimuli/prepare for certain actions, thus they must have made a prediction) in violation paradigms (comparing highly expectable to less predictable input, cf. Federmeier, Kutas, & Schul, 2010; Wlotko, Federmeier, & Kutas, 2012), thus the evidence for predictive language processing remains indirect. In the mammalian brain, spatial prediction was demonstrated in form of reoccurring neuronal firing patterns: After being familiarized to a specific maze, rats display approximately the same firing sequences prior to going into the same maze again that they had exhibited while actually running through the maze before (Diba & Buzsaki, 2007). The present project aimed at making linguistic predictions observable by developing a new “predictive eye gaze reading task”: Word sequences (always missing the final word) were presented visually. The final target word was displayed with a delay of approximately five seconds at a specific position on the screen, depending on its syntactic categories; the participants were asked to judge whether or not the target word was a grammatically valid continuation of the previous word sequence. During the delay before the target word was presented, anticipatory eye movements into the respective expected target location were assessed, providing insights about the existence and the timing of linguistic predictions. This timing information in turn informed the fMRI model in order to extract the neural substrate of linguistic predictions.

However, when assessing the brain correlates of linguistic predictions, it is important to differentiate between language aspects a prediction could be based on. Two important constituents of language are reasonable candidates: syntax and semantics. In consequence, the first prediction study reported in the present thesis incorporates three conditions: (1) normal sentences, where predictions are possible based on both sentence structure and semantics, (2) meaningless jabberwocky sentences, where the participant is able to generate a prediction regarding the word category of the delayed final word, but cannot anticipate a specific word, and (3) non-word lists, where no prediction is possible. However, as those conditions do not reveal predictive processing purely based on semantics, an additional study investigated sequences of content words and non-words that allowed predicting the semantic category of the final word. This purely semantic prediction was again compared to predictions in the context of normal sentences and a control condition without predictive processing (i.e., non-word lists). The two respective eye tracking pilot studies (cf. sections 2.4.2 and 2.4.3) revealed that participants indeed anticipated the syntactic and semantic category of target words in normal sentences, the syntactic word category in meaningless jabberwocky sentences and the semantic category in pure semantic conditions; however – as expected – they failed to generate reliable predictions in non-word lists. Thus, given a successful task that triggers and reveals linguistic predictions, it was possible to investigate the neural substrate of predictive processes in language.

1.2.2 HYPOTHESES

The linguistic prediction hypotheses need to cover three aspects: (a) Behavioral performance in the grammaticality judgment task, (b) the timing and the accuracy of the anticipatory eye-movements, and (c) the neurophysiological activation pattern induced by linguistic predictions. Starting with anticipatory eye movements and behavioral performance, the hypotheses are straightforward:

1. Participants should only generate word category predictions (as indicated by anticipatory eye gazes) and judge the grammaticality of the target words correctly (i.e., above chance level) in the context of sentences and meaningless jabberwocky sentences, but not in non-word lists.
2. Participants should only generate semantic predictions (as indicated by anticipatory eye gazes) and judge the semantic acceptability of the target words correctly (i.e., above chance level) in the context of sentences and semantic sequences, but not in non-word lists.
3. Combined syntactic and semantic – as opposed to purely syntactic – predictions (i.e., the possibility to predict a specific word) should improve the quality of the prediction, thus enhancing the speed and certainty of the anticipatory eye movements for the correct target word area and additionally improving grammatical judgments.

Regarding the neurophysiological correlates of the predictive linguistic processing, the literature is sparse. Following the logic of predictive coding, our brain generates predictions of what is likely to be perceived next based on stored cognitive models built from past experiences. The same areas involved in processing a specific stimulus type are also assumed to be involved in generating a respective prediction. Which brain systems might support a prediction in the linguistic domain?

A first candidate for word category prediction in both meaningful and meaningless (i.e., jabberwocky) sentences are brain systems supporting structural *syntactic processing* (such as Broca's area, frontal operculum, caudate nucleus, and thalamus; Jeon, Anwander, & Friederici, 2014). Additionally, the ventral premotor cortex has been implicated in syntactic processing and has been argued to support the sequential mapping onto structural (i.e., syntactic) templates (Bahlmann, Schubotz, & Friederici, 2008; Fiebach & Schubotz, 2006; Opitz & Kotz, 2012). When predicting semantic categories or specific words, we might additionally recruit the *semantic system* (including areas such as e.g. the middle temporal lobe and the inferior parietal lobe; for a comprehensive review see Binder et al., 2009). Moreover, studies by Dikker and colleagues suggest that predicting the visual form of a concrete word might lead to an activation of the visual cortex (Dikker & Pylkkanen, 2011; Dikker et al., 2010; Dikker et al., 2009). The authors report that the M100 (i.e., a magnetencophalographic component reflecting manipulation of lower level visual features) is sensitive to the syntax-induced predictability of a word form. As the M100 has been localized in the occipital lobe (i.e., the medial portion of the lingual gyrus, the cuneus, and the primary visual cortex bilaterally; cf. Itier, Herdman, George, Cheyne, & Taylor, 2006), involvement of the visual system in generating a word prediction is hypothesized in the present study. Moreover, the visual word form area (located in the left fusiform gyrus, cf. McCandliss, Cohen, & Dehaene, 2003) is another possible candidate for supporting the prediction of a specific word, whereas it is not expected to be involved in a pure word category prediction that does not allow anticipating a specific word and its visual form.

On a more general account, predicting words or word categories means to predict successive elements of a sequence, thus more domain-general systems involved in various types of *sequential processing* are additional possible candidates for supporting linguistic predictions. For example, the hippocampus has been reported to code for sequences of neuronal firing patterns and the calculation of prediction errors (Lisman & Redish, 2009; Schiffer, Ahlheim, Wurm, & Schubotz, 2012; Tubridy & Davachi, 2011) and for predictive processes in animal research across domains (Diba & Buzsaki, 2007; Lisman & Redish, 2009).

In summary, the second major objective of the present thesis was to investigate predictive processes in language and to study their neural underpinnings in the domain of visual sentence processing. In line with the general proposal of predictive coding (which suggests that the brain is predictive in nature, using the same brain systems for processing and predicting input), areas supporting the online processing of language (syntax, semantics) and regions involved in sequence processing across domains are regarded potential candidates for the generation of linguistic predictions.

1.3 CONNECTING PREDICTION TO MEMORY IN SENTENCE PROCESSING

Obviously, prediction processes are far from independent of memory: Predictions are built based on previous experiences, thus they highly depend on the availability of memory contents (see e.g. Bar, 2007, 2009; Buckner, 2010; Mullally & Maguire, 2014; Schacter, Addis, & Buckner, 2007; Schacter et al., 2012). Already in the early 1990ies, Paul van den Broek proposed in his process model of text comprehension (i.e., “the causal inference maker”, van den Broek, 1990, 1994) that comprehending a narrative at times leads the reader to build forward inferences. Consider the following example (van den Broek, 1994; p. 572):

1- *While shooting a film, the actress accidentally fell out of the first floor window.*
2- *While shooting a film, the actress accidentally fell out of the 14th floor window.*

General knowledge about what happens to objects falling to the ground from very high heights suggests that in example 2, the actress died (i.e., a predictive inference is generated). Based on the observation that predictive inferences rely on memory, two studies investigated whether or not the generation of predictive inferences during reading depends on the individual working memory capacity of the reader (Estevez & Calvo, 2000; Linderholm, 2002). In the study by Linderholm (2002), participants were assigned to a high or low working memory capacity (WMC) group based on their reading span; both groups were tested for their ability to generate predictive inferences. For example, after being presented with a highly constraining context such as "Patty bit into the apple, then stared at it. It had half a worm in it.", subjects were asked to pronounce a probe word ("SPIT"). The naming times were compared to conditions with a low or moderate constraining context (e.g., "Patty bit into the apple, then stared at it. It had little flavor."). Indeed, participants with high WMC named the probe word faster in the highly predictive context, whereas the low working memory capacity group did not. Other experiments indicated that low WMC individuals actually show signs of predictive inferences, if they are given sufficient time (Estevez & Calvo, 2000; Linderholm, 2002, second experiment).

These studies thus link working memory to predictive inferencing; however, one must differentiate between a predictive inference (i.e. anticipation of future events based on implicit, indirect causal implications of a text) as proposed by van den Broek and the prediction of upcoming words in a sentence investigated in the present thesis:

1. *Predictive inference: While shooting a film, the actress accidentally fell out of the 14th floor window.* → *[the actress died]*
2. *Word prediction in sentence processing: Er wollte das wilde Pferd ohne Sattel* → *[reiten]*[3]

Predictive inferences are assumed to be resource-demanding and time-consuming, whereas the prediction of a target word in the context of a highly predictive (i.e., semantically and syntactically constrained) sentence or discourse might be a faster and automatic process (e.g. Federmeier et al., 2010; Lau et al., 2006). However, both types of linguistic prediction rely on existing knowledge that has to be readily available during reading, raising again the question of shared neural resources for word prediction and memory processes. Therefore, results from memorizing and prediction processes are integrated in chapter 5.3.

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[3] Literal translation to English: "*He wanted the wild horse without saddle* → [*to ride*]"

1.4 SUMMARY AND OVERVIEW

During conversations, online linguistic processing of your interlocutor's utterances alone is not sufficient, especially if you want to engage in a discourse. Instead you have to keep track of the preceding conversation contents while simultaneously handling vast amount of incoming information. Complying with these demands relies on reliable and efficient memorizing and might be improved by a proactive predictive linguistic processing.

The former part, namely the efficient memorizing of sentences, represents the first scientific focus of the present thesis. Investigating the influence of sentence structure on working memory load and rehearsal strategies required a careful experimental design and a new stimulus set; the stimulus generation as well as the behavioral pilot study evaluating the paradigm are detailed in chapter 2.4.1. After demonstrating the validity of the paradigm, the investigation of the brain processes underlying a better recall of sentences compared to ungrammatical word lists is described and discussed in chapter 0 (chapter corresponds to the article published in the Journal of Cognitive Neuroscience; Bonhage et al., 2014).

The second part of the thesis is concerned with predictive processes in language. As described in the previous section, proactive predictive processing is assumed to boost online language processing; however measuring predictions remains an experimental challenge: Which task allows observing a predictive process online, indicating its existence and - importantly - its timing? The two versions of the new predictive eye movement reading task created to comply with the above mentioned requirements are detailed in section 2.4.2 and 2.4.3, including the generation of the stimulus sets as well as the respective behavioral and eye tracking pilot studies. The investigation of the neural substrates of linguistic predictions is delineated in the manuscript in chapter 4[4].

Ultimately, results from both memorizing and predictive processes in language are integrated and discussed in the context of state-of-the-art neurolinguistic theories in chapter 5. A final analysis aims at identifying a shared network of regions involved in both types of processes, providing evidence for a neurophysiological connection between memory and prediction processes in language.

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[4] Chapter corresponds to the submitted manuscript (preprint) of Bonhage, C. E., Mueller, J. L., Friederici, A. D., & Fiebach, C. J. (2015, in press). Combined eye tracking and fMRI reveals neural basis of linguistic predictions during sentence comprehension, *Cortex*, http://dx.doi.org/10.1016/j.cortex.2015.04.011.

2 GENERAL METHODS

The following chapter sheds light on the experimental methodologies used to answer the research questions of the present thesis, covering behavioral and electrophysiological measures as well as eye tracking and functional magnet resonance tomography.

2.1 BEHAVIORAL MEASURES

To investigate a cognitive process in an experimental setup, the most common approach is to give the participants a task that requires engagement in the respective cognition of interest and measure their responses. In this context, behavioral measures can serve two functions: First, it is a proper way to provide evidence that the participant actually worked on the task and thus executed the cognitive process the experimenter aimed to investigate. Second, the accuracy of the responses and the response speed of the participants indicate the difficulty of the task, because in easier tasks, participants tend to react faster and more reliable. Notably, those measures are dependent: Although a task may be very difficult, high accuracy nevertheless can be achieved by compensating with prolonged response times.

In all of the experiments conducted during the present dissertation, participants were required to perform a two-alternative forced choice indicating a yes/no-response via button press. Those button presses, more specifically the response time and the accuracy of each response were recorded using the stimulus presentation software Presentation® (Neurobehavioral Systems, www.neurobs.com). Responses were given with the thumbs of each hand (e.g. left thumb = “yes”, right thumb = “no”). Due to enhanced response times in the dominant hand compared to the non-dominant for left- and right handers and because of the known lateralization differences in the brains of left- and right-handed humans in language processing (cf. Goodin, Aminoff, Ortiz, & Chequer, 1996), only right handers were invited to participate. The assignment of thumbs to yes/no-responses was counterbalanced across participants in each of the experiments.

2.2 EYE TRACKING

To answer the second major research question of the present thesis (i.e., how predictive processes are mirrored in the brain), a new experimental design was created, using anticipatory eye movements as indicators for the existence and the timing of linguistic predictions. The following section seeks to explain why eye tracking is widely considered a powerful objective measure for investigating cognitive processes by providing a short introduction to the eye tracking technique based on the books of Horsley, Eliot and Knight (*Current Trends in Eye Tracking Research*, 2014), Duchowski (*Eye Tracking Methodology - Theory and Practice*, 2007), and Sundstedt (*Gazing at Games: An Introduction to Eye Tracking Control*, 2011).

In general, visual paradigms conducted in Cognitive Science require the participants to use and react to visual information. Participants direct their gaze at those parts of the experimental setup that provide useful information while relocating their foveae approximately three times per second without being aware of it (Tatler, Kirtley, Macdonald, Mitchell, & Savage, 2014). Importantly, changes of gaze direction from one informative point to another are unconscious; thus in careful experimental designs eye tracking can reveal the cognitive processes underlying the participants' behavior in experimental settings. This has been demonstrated numerous times across different domains, for instance in linking action and perception (i.e., eye movements that precede, accompany and follow actions in order to guide behavior and receive feedback; see e.g. Fagioli, Hommel, & Schubotz, 2007; Hommel, Musseler, Aschersleben, & Prinz, 2001), investigating what people focus on during social interactions (e.g. Laidlaw, Foulsham, Kuhn, & Kingstone, 2011), but also in the linguistic domain investigating people during reading processes in various languages (e.g. Betancort, Carreiras, & Sturt, 2009; Knoeferle & Crocker, 2009; Lee, Lee, & Gordon, 2007; for an overview of older literature, see Rayner, 1998). In the present study, the scope of application is extended by measuring *anticipatory* eye movements during language processing.

Eye tracking recordings. Eye tracking is a technique that allows to record eye movements in real time. In classical computer-based eye tracking experiments the researcher aims to reconstruct which screen positions the participants were fixating throughout the experiment (e.g. Bax, 2013; Vandeberg, Bouwmeester, Bocanegra, & Zwaan, 2013). Technically, all eye trackers used during the present thesis record the gaze coordinates as well as the pupils size by sending out light pulses in the near infrared spectrum and measuring the respective reflection as well as the pupil size with an integrated camera, combining information gathered by on-axis (i.e., bright-pupil) and off-axis (i.e., dark-pupil) tracking (behavioral pilot study of the project investigating working memory for sentences, section 2.4.2: Tobii X120, Tobii Technology GmbH, www.tobii.com; fMRI experiment of the syntactic prediction project, section 4: Applied Science Laboratories (ASL) long range eye tracker[5], MRI compatible, www.asleyetracking.com; behavioral study investigating semantic predictions, section 2.4.3: Tobii T120, Tobii Technology GmbH, www.tobii.com). On-axis tracking is achieved when both camera and illumination source are on the same axis, thus an illuminated pupil is recorded

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[5] www.asleyetracking.com/Site/Products/EYETRACPC/fMRIAndMEG/tabid/69/Default.aspx

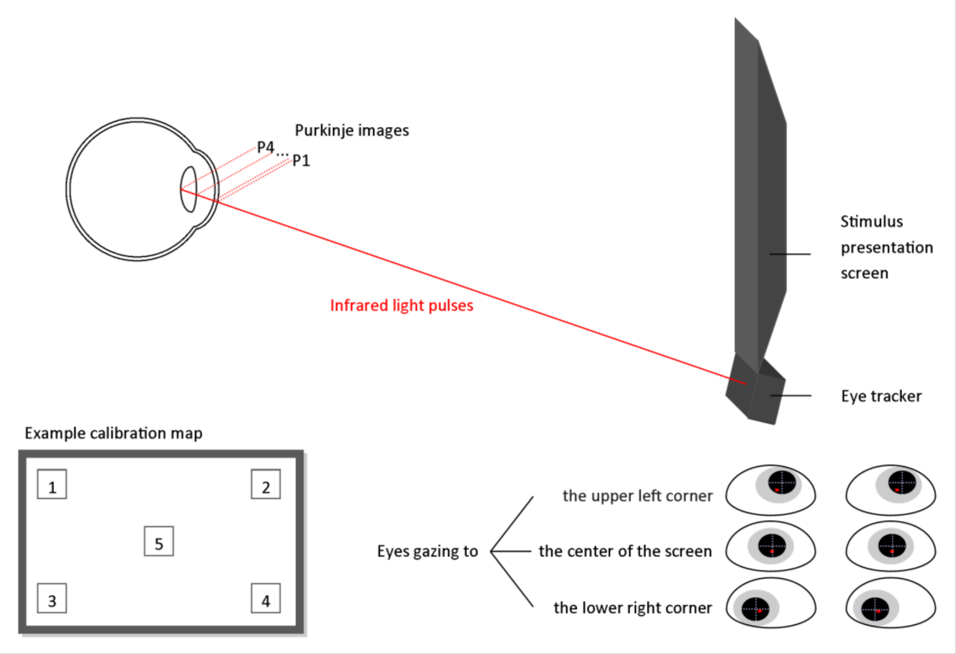


Figure 2-1: Eye tracking method and calibration.

(an effect similar to the "red-eye effect" when using a flash in photography, cf. Weigle & Banks, 2008). In contrast, off-axis tracking requires the camera not to be on the same axis, and it produces dark pupils. Taken together, these measures provide a very accurate outline of the pupil, which then can be used to calculate its center. However, to measure the gaze position, information about the pupil outline is not sufficient; the cornea reflection is needed additionally. The infrared pulses are reflected off the eye structures differentially, thereby creating four Purkinje images (PI 1-4, cf. Figure 2-1).

A common way to extract the eye movement is to calculate the vector difference between the center of the pupil and the first PI (i.e., the anterior corneas' reflection) depending on the fixation point. This fixation point is varied systematically during the calibration procedure: Before starting an experiment, the eye tracking system has to be calibrated to each participant's eyes. In our case, a 5-point (Tobii system, behavioral studies) or a 9-point (ASL long range system, fMRI experiment) calibration was conducted for each subject: The participant was asked to fixate five or nine predefined locations on the computer screen; the angular positions of those locations are known (cf. Figure 2-1). Samples of pupil-to-PI vectors were saved for each of those positions. As described above, the location of the cornea reflection within the dark pupil differs depending on the location the participant is fixating (cf. Figure 2-1). Based on the respective vector information acquired during calibration, the eye tracking system is able to perform a back-computation of the participants' gazes throughout the experiment (for more extensive information, see Hansen & Ji, 2010).

Understandably, an individual and exact calibration procedure preceding the experiment is vital to obtain valid eye tracking data. In the present eye tracking systems, both the exact x/y-coordinates of the gaze and the pupil size were saved at a rate of 60 Hz. Combined with a conventional stimulus presentation software such as Presentation®, the experimenter is able to reconstruct during which parts of the experiment and for how long the participant has been gazing at which part of the screen.

Analysis of eye tracking data. Output of the eye tracking system (besides the distance of the eyes to the camera, the time stamp of measurement and the validity of the gaze data) are parameters such as the x/y-coordinates of the eye gaze and the pupil size throughout the experiment. For analysis purposes, the experimenter can define regions of interest (defined in x/y-coordinates) and compute several parameters, for example the fixation time of a specific area or the time it takes the participant to move his/her eyes from one location to another location (i.e., saccade duration, first look). The exact statistical analysis of the resulting eye tracking parameters is described for each experiment individually in the respective sections of the thesis (i.e., sections 2.4.1, 2.4.2, and 2.4.3).

To sum up, in the experiments conducted over the course of the present PhD thesis eye tracking was used to assess anticipatory eye gazes during predictive processes in language comprehension. However, since the focus of the research question was not only to deliver evidence for the existence of linguistic predictions, but also to investigate the neural networks supporting these predictions, a neurophysiological method was applied additionally. Accordingly, the following sections will describe the basic mechanism of functional magnetic resonance imaging.

2.3 FUNCTIONAL MAGNETIC RESONANCE IMAGING (FMRI)

Developed only roughly 20 years ago, fMRI has arisen to one of the most popular techniques in neuroscience. Non-invasively, researchers acquire series of brain images while participants engage in a task. The basic fMRI rational presumes that during a task, the neuronal activity changes in task-relevant brain areas. These changes are assumed to lead to a change in metabolism within the respective area, which can be represented in the MR images. If the changes are consistent over many trials of the same cognitive task, fMRI statistics allow determining the brain areas supporting the respective task. Compared to MEG and EEG, fMRI offers a very low sampling rate, but stands out with a high spatial resolution. The following section is based on the textbooks of Faro and Mohamed (*Functional MRI - Basic Principles and Clinical Applications*, 2006), Frakowiak et al. (*Human Brain Function*, 2004), Huettel, Song and McCarthy (Functional Magnetic Resonance Imaging, 2009a) and Stroman (*Essentials of Functional MRI*, 2011), and covers the basic concepts of the fMRI technique, describes its signal sources and briefly touches on the computational methods to preprocess fMRI data. The exact statistical approaches used in the present experiments are detailed in the respective chapters of the thesis.

Basic concepts. The MR system is designed to create a static magnetic field B_0, homogeneous in strength and direction. The field strength used in conventional human MR scanners ranges from 1-10 Tesla; stronger magnets generate a higher signal-to-noise ratio by producing an enhanced signal. In general, running an electrical current through a wire creates a magnetic field around it. In the center of a loop of wire the magnetic field is homogeneous, for this reason the main coil of the MR scanner is constructed by ordering many loops of superconducting wire in a cylindrical shape, spaced to generate the homogeneous three-dimensional magnetic field B_0 inside. However, placing any type of material (e.g. the head of the participant) within B_0 slightly changes the field. In order to be able to re-establish the homogeneity of B_0, built-in magnetic field gradients in x- y- and z-direction inside the main coil allow for 'active shimming'. Active shimming refers to a two-step procedure: First, the static magnetic field with the material inside is mapped; afterwards the electrical current needed to re-establish homogeneity is computed for and applied to each gradient separately. This procedure is necessary every time an object is explored with MRI.

Sources of MRI signal. In order to assess a brain process using the MRI technique, it is essential to be aware of the origin of the acquired signal. In general, the MR system makes use of the magnetic properties of the nucleus of the hydrogen atom (^1H), which is largely available in human tissue (mostly in water, H_2O, but also in certain lipids; both are important components of neural tissue). The hydrogen atoms' nucleus is composed of a single proton spinning around its axis. Outside the static magnetic field of the MR scanner (B_0), the protons are oriented in a random fashion; therefore the individual magnetization of the protons on average cancels out. The MR system circumvents this cancel-out effect by establishing B_0, which forces the protons to align in a parallel or antiparallel manner. However, to assess the net magnetization of the nuclei, the direction of the magnetization has to be changed. To this end the MR system provides not only the static and homogeneous magnetic field B_0, but also radio-frequency (RF) magnetic fields produced by RF coils around participants' head. The RF fields oscillate (i.e., rotate) at high frequencies due to rapid changes in the direction of the electrical current running through the RF coils. Whenever the direction of the magnetic field is changed at an angle of approximately 90°, the protons' equilibrium state (i.e., in their ordered state within B_0) is disturbed and, forced by the new orientation of the magnetic field, they precess to the according direction. As soon as the RF field is switched off, the proton spins realign to their original equilibrium position, leading to a change in the net magnetization which is detected by the receiver coils. Different tissue types and fluids have a different proton density; the resulting information is translated into false colors, producing the well-known structural brain images. However, different types of MR sequences are sensitive to different sorts of magnetizable material; for example, the structural scans are acquired in T_1 or T_2 contrasts (sensitive to tissue and fluid-filled regions, respectively).

Functional MRI (fMRI) - assessing metabolism in the brain. To extract the brain areas involved in a cognitive task, the metabolism processes induced by neuronal activity are captured by a contrast sensitive to the oxygenation state of the hemoglobin, T_2*. T_2*-weighted images reflect the duration of the transverse relaxation of the proton' spin after the RF pulse into the original direction of B_0, which is caused by spin-spin-interaction between protons (T_2) and the changing spin precession frequencies induced by inhomogeneities in the magnetic fields. To estimate a T_2* contrast, the pulse sequence is characterized by a long delay between successive RF pulses (i.e., repetition time, TR) and a medium delay between the RF pulse and the MR image acquisition (i.e., echo time, TE).

The studies described in the present work investigated the neurophysiological responses to linguistic tasks. Given that participants engage in a task while lying in the scanner, the fMRI technique is acting on the assumption that neuronal firing needs energy, leading to an enhanced metabolism within the brain areas responsible for task completion. One essential prerequisite for metabolism is the availability of oxygen, which is carried by hemoglobin molecules. Hemoglobin, part of the red blood cells, inherits its magnetic properties from its iron nucleus. The magnetic properties change when the oxygen is released: While desoxygenated hemoglobin is paramagnetic, oxygenated hemoglobin is characterized by a far smaller magnetic moment. As soon as neurons start to fire, a first initial dip in oxygen concentration can be detected; however afterwards more oxygen is brought in than consumed by metabolism (i.e., overcompensation). In consequence, the proportion of oxygenated hemoglobin compared to desoxygenated hemoglobin is higher, altering the net magnetization within the respective brain area. This contrast is called blood oxygenation level dependent (BOLD) contrast (cf. Ogawa, Lee, Kay, & Tank, 1990).

However, as the brain is not fully occupied by the experimental task but serves many other, mostly unconscious processes (e.g., establishing homeostasis) at the same time, it is essential to repeat the task several times in order to statistically estimate which brain areas display a metabolic activity that varies consistently with the experimental task (i.e., increase the signal-to-noise ratio).

Experimental procedure. A typical fMRI session starts with a short localizer sequence that assesses the head position of the participant lying in the scanner, followed by active shimming (as described above) to establish the homogeneous static magnetic field B_0. Afterwards, a high-resolution structural scan of the brain is acquired. This structural scan is a necessary step, because the functional (i.e. echo planar imaging, EPI) sequences used during the functional scans only provide very low resolution brain volumes. The low resolution enables a fast acquisition, which is necessary to track the hemodynamic response curve induced by the cognitive process. Afterwards, the high-resolution structural scan of the participants' brain allows mapping the activity patterns extracted from the functional scans to the original structural scan; thereby providing a more detailed insight about their exact location (i.e., coregistration).

Statistical analysis. Before statistical analyses on individual or group level can be performed, MRI data has to undergo several preprocessing steps. The fMRI community provides a wide range of ways to prepare neuroimaging data for statistical analysis; because describing all of them in detail would certainly extend the scope of this section, the dedicated reader is relegated to Huettel, Song, and McCarthy (2009b) for further reading. This section focusses on the preprocessing steps performed over the course of the present fMRI experiments.

Functional MRI data collection is done sequentially, acquiring 30 slices (i.e., 2D images) per brain volume in the present studies within a TR of two seconds. Therefore the temporal delay between the slices belonging to a specific brain volume (i.e., slice-time correction) has to be taken into account. Additionally, motion artifacts have to be considered; to this end, all brain volumes are coregistered to a single registration volume, calculating the mutual information and spatially interpolating the data to estimate fMRI data without head movement. Afterwards, the functional data is coregistered to the structural images to obtain a higher spatial resolution. A final step before statistical analysis is spatial normalization. Because the morphology between human brains varies remarkably, fMRI preprocessing has to compensate for the individual differences in size, shape and organization of gyri and sulci. Therefore, all individual data is normalized into a common stereotactic space (i.e., MNI space, provided by the Montreal Neurological Institute) to enable group-level fMRI analyses.

To sum up, fMRI allows extracting the brain regions supporting specific cognitive processes by observing hemodynamic changes that are correlated to the respective cognition. As now all methods used in the present experiments are introduced to the reader, the following sections will continue by describing all pilot studies conducted in preparation for investigating the neural basis of memorization and prediction processes.

2.4 BEHAVIORAL (PILOT) STUDIES

After the basic introduction to the research methods, the following section covers the behavioral studies preceding both fMRI studies reported in the manuscripts in chapter 0 and chapter 4. As both studies relied on new experimental designs, the creation of new stimulus sets was required; the respective stimulus creation, selection, and behavioral piloting will be detailed below.

2.4.1 PROJECT 1: REMEMBERING SENTENCES VERSUS UNGRAMMATICAL WORD SEQUENCES

As described in section 1.1, sentences are easier to recall than ungrammatical word strings, but it remains unclear, which brain processes underlie this alleviation process over the first consecutive stages of memorizing (i.e., encoding and maintenance of information). The present study thus investigated neuronal and behavioral effects of working memory load and sentence structure – as well as their dependence on rehearsal processes during the maintenance of word sequences. In consequence, the stimulus set for the present working memory study required grammatical (i.e., with sentence structure, SST+) and ungrammatical (i.e., without sentence structure, SST-) word sequences in both a low (loWML) and high (hiWML) working memory load version. Those stimuli were presented twice, once allowing the participant to rehearse the items while maintaining them in memory (in the absence of Articulatory Suppressing, AS), once without rehearsal options (including AS).

2.4.1.1 Stimulus Creation and Pretest of Stimulus Set

An original set of 60 items was created using German four-word sentence fragments such as “er hat sie von” (cf. Figure 3-1). To additionally gain a high load version of the same stimulus, we added two words to each four-word string, in our example “er hat sie gestern Abend von”. This long and short version of a grammatically correct sentence fragment were now reordered into an ungrammatical order such as “er von hat Abend gestern sie”, trying to exclude as many grammatical serial combinations of words as possible, resulting in short and long versions of ungrammatical items that contained the exact same words as their grammatical counterparts.

Pretest and stimulus selection. All 60 original stimulus quadruples (i.e., a low and a high WML version of a matched grammatical and ungrammatical word string, resulting in a total of 240 original items) were presented to participants in an online questionnaire (using the open source survey application LimeSurvey, www.limesurvey.org) in a randomized order. Twenty-one participants (11 female, mean age = 25.8, age sd = 2.9) were instructed to rate the grammatical acceptability of each item in an online survey. Participants were compensated with seven Euros per hour. The final set of 30 stimulus quadruples (120 items in total) was selected by accepting items that had a very high grammatical acceptability (mean = 98.1%; sd = 4.7) in the grammatical word sequences and a very low acceptability (mean = 1.7%; sd = 2.8) in the ungrammatical word sequences in both load versions.

2.4.1.2 Behavioral pilot study

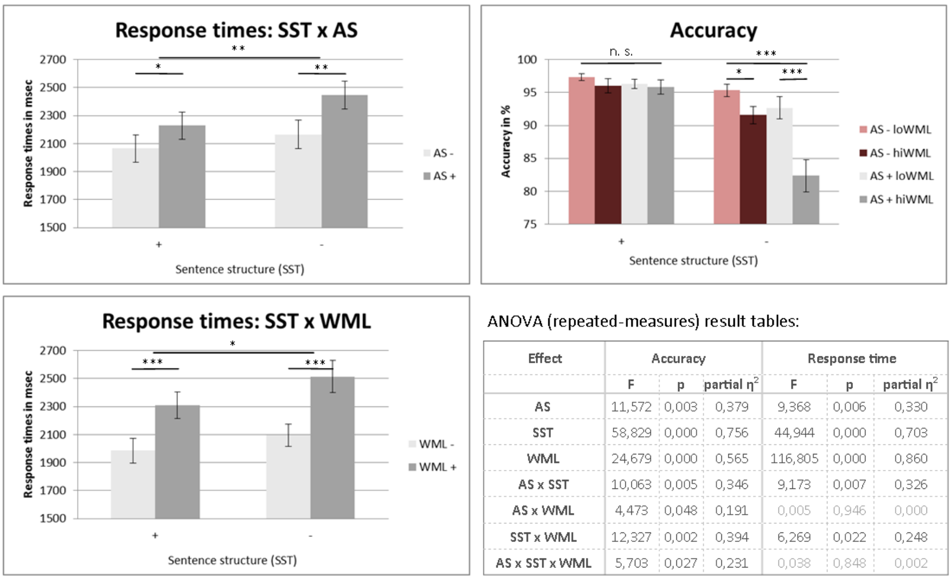
As not only the (un)grammaticality of the items, but also a behaviorally significant load effect of longer word sequences (as indicated by a decreased performance in hiWML) in ungrammatical word strings was vital to the present paradigm, the items were tested in a behavioral pilot experiment. Simulating the subsequent fMRI study, the stimulus presentation software Presentation® (Version 14.1, www.neurobs.com) was used to obtain data from 20 German natives (10 female, mean age = 23.4; sd = 2.4). All participants took part in two one-hour sessions of the behavioral pilot study after receiving extensive information and instruction in line with the Declaration of Helsinki (Version of 2008, www.wma.net/en/30publications/10policies/b3/); in order to reduce memory benefits for session II, the sessions were conducted on separate days with a minimum of five days in between. Participants were compensated with seven Euros per hour.

As briefly mentioned above, all 120 items were presented twice: In one session, participants were allowed to rehearse the items during the maintenance phase (i.e., without Articulatory Suppression, AS-); the other session included Articulatory Suppression (AS+). AS, as introduced in the General Introduction, refers to a technique that requires participants to vocalize unrelated material during a memory task (in the present study's case the nonsense syllable string "nena dana nena dana …"); by this vocalization (sub-)vocal rehearsal is prevented (Hanley & Thomas, 1984; Murray, 1968). In order to keep articulation rates between participants constant, each "nena dana" vocalization was paced by a reoccurring fixation cross (every second). The order of AS sessions (AS+, AS-) was counterbalanced across participants. Additionally, to ensure that participants would not try to re-order ungrammatical word sequences into grammatical ones, the experimental task required participants to remember the words in the serial order of their appearance. Specifically, after the maintenance period, participants were asked whether a specific word A from the preceding word sequences was presented before a specific word B. Participants responded via button press on a response box with two buttons ("yes" and "no"). After a short training block to familiarize participants with the present task, participants were challenged with the working memory task for approximately 50 minutes, with a break after half of the stimuli.

To judge whether the present paradigm successfully induces the beneficial effects of SST as well as the detrimental effects of WML and AS, three hypotheses were formulated. First, participants were expected to respond faster to stimuli with a correct grammatical structure compared to ungrammatical items (i.e., SST+ < SST-). Second, both hiWML and AS+ were hypothesized to slow down response times. Third, the accuracy was assumed to drop in SST-, hiWML, and AS+ as compared to SST+, loWML, and AS-, respectively. However, the effects of hiWML and AS+ were expected to be reduced in grammatical items (SST+).

Analysis and results. Response times and accuracy of responses were recorded in the stimulus presentation software Presentation® and statistically analyzed using PASW 19 (SPSS Inc., www.spss.com.hk/statistics). Two general linear models (repeated-measures) were estimated, investigating the response times and accuracies of participants depending on the within-subjects factors SST, WML, and AS (cf. Figure 2-2). Focusing on the *response times* first, the response times were significantly influenced by WML and AS in both grammatical (SST+) and ungrammatical (SST-) conditions. Post-hoc comparisons investigating the interaction between SST and AS as well as the interaction between SST and WML revealed two major findings: First, a response time difference between AS+ and AS- reached statistical significance in both SST+ (t(19) = -2.263; p=0.036) and SST- (t(19) = -3.608; p=0.002); however the difference in RTs between AS+ and AS- items was larger in SST- than SST+ (t(19) =-3.029, P=0.007). Second, the same was true for WML: Although the RTs were significantly slower for hiWML+ than loWML in both SST+ (t(19) = -11.934, p <0.001) and SST-(t(19) = -8.622, p <0.001) items, the decrease in RT was again larger in SST- than SST+ (t(19) =-2.50; p=0.022). Taken together, the findings strongly suggest a beneficial effect of sentence structure on RTs particularly under difficult working memory conditions (i.e., hiWML and AS+).

In contrast, as long as sentence structure was provided (i.e., SST+), the *accuracy* of responses did not significantly differ between the levels of WML and AS: A reduced GLM (repeated measures) of AS*WML in SST+ conditions revealed that neither the main effect of AS (F(1,19) = 0.671, p = 0.423) or WML (F(1,19) = 0.992, p = 0.332) nor the interaction between those factors (F(1,19) = 0.294, p = 0.594) reached significance. However, as soon as sentence structure was taken away (i.e., SST-), the detrimental effects of more material (hiWML) and AS (AS+) on accuracy were evident (main effect of AS, F(1,19) = 12.847, p=0.002; main effect of WML, F(1,19) = 25.351, p < 0.001; interaction AS*WML, F(1,19) = 6.919, p = 0.016). Specifically, in SST- items a WML effect is present under both AS+ (t(19) = 4.788, p < 0.000) and AS-



ANOVA (repeated-measures) result tables:

Effect	Accuracy			Response time		
	F	p	partial η^2	F	p	partial η^2
AS	11,572	0,003	0,379	9,368	0,006	0,330
SST	58,829	0,000	0,756	44,944	0,000	0,703
WML	24,679	0,000	0,565	116,805	0,000	0,860
AS x SST	10,063	0,005	0,346	9,173	0,007	0,326
AS x WML	4,473	0,048	0,191	0,005	0,946	0,000
SST x WML	12,327	0,002	0,394	6,269	0,022	0,248
AS x SST x WML	5,703	0,027	0,231	0,038	0,848	0,002

Figure 2-2: Behavioral results of the pilot study investigating working memory for sentences. AS, Articulatory Suppression (AS-, without; AS+, with); SST, sentence structure (SST+, grammatical word order; SST-, ungrammatical word order); WML, working memory load (loWML, low load; hiWML, high load).

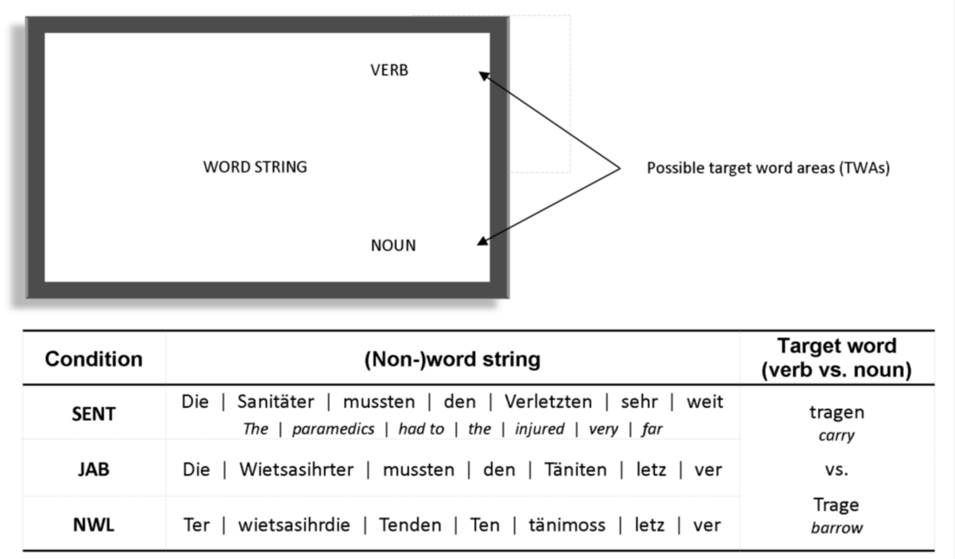
(t(19) = 2.443, p = 0.024) conditions, while a disadvantageous effect of AS is observable only in high load items (t(19) = 3.823, p = 0.001), but not in low load items (t(19) = 1.595, p = 0.127).

To sum up the results of the behavioral pilot study, the present paradigm elicits the detrimental effects of high WML and AS. Furthermore, it provides evidence for the sentence superiority effect (SSE): The memory performance for word strings with sentence structure is enhanced compared to ungrammatical word strings. Taken together, the behavioral results indicate that the present experimental design and materials are well suited to investigate the sentence superiority effect and its underlying neural processes, and disentangle it from pure load effects or rehearsal mechanisms. Subsequently, a functional magnetic resonance imaging (fMRI) study was conducted, described in the first manuscript included in the thesis (section 0).

Following this extensive investigation of syntax-driven memory facilitation effects, the second major research question of the thesis is concerned with linguistic predictions. The following two sections provide an overview over the creation of the experimental design and materials as well as the behavioral piloting of syntactic and semantic predictions experiments.

2.4.2 PROJECT 2: PREDICTING WORDS AND SYNTACTIC CATEGORIES

As pointed out in section 1.2, language processing can be speeded up dramatically if one assumes predictive mechanisms during comprehension. To measure predictions of meaningful words and syntactic categories, a new experimental design was developed. Note that although it is quite appealing to theoretically argue for the existence of predictions, it is rather challenging to prove experimentally, that a specific predictive process has taken place at a specific time during the experiment. To solve this issue, eye tracking was used to make the prediction process accessible to observation: Specific syntactic categories (verb vs. noun) were associated with specific locations on the computer screen (upper vs. lower right corner, cf. Figure 2-3). The rational goes as follows: In order to trigger syntactic expectancies in participants, word sequences (e.g., normal sentences) are presented word by word in the center of the screen, missing only the sentence final word. At this point, participants should develop a clear prediction regarding the word category of the final word. The final (i.e., target) word is presented with a delay of ~3 seconds (i.e., after the prediction phase). In anticipation of the grammatically valid target item, participants are expected to shift their eye gaze from the center of the screen into the respective target word area. For example, if participants expect a verb at the end of the sentences, they are expected to move their eyes into the upper right corner



Condition	(Non-)word string	Target word (verb vs. noun)
SENT	Die | Sanitäter | mussten | den | Verletzten | sehr | weit *The | paramedics | had to | the | injured | very | far*	tragen *carry*
JAB	Die | Wietsasihrter | mussten | den | Täniten | letz | ver	vs.
NWL	Ter | wietsasihrdie | Tenden | Ten | tänimoss | letz | ver	Trage *barrow*

Figure 2-3: Association of screen location and target word category, experimental design and item example (literal translation to English provided in italics; note that the word order in the SENT condition is grammatically correct in German). SENT, normal sentences; JAB, jabberwocky sentences; NWL, non-word lists.

before the target word appears. These anticipatory eye movements – if displayed by the participants – would provide strong evidence for the existence of a predictive process.

The ultimate goal of the syntactic prediction project was to extract the neural resources underlying the prediction of a specific word (i.e., based on syntactic structure *and* semantic content in the context of normal sentences; cf. Figure 2-3) and compare those to a condition in which a prediction can be made regarding the syntactic category, but not regarding the semantic content of the target word (i.e., in the context of meaningless jabberwocky sentences). In jabberwocky sentences, function words were retained while content words were exchanged with pronounceable non-words. Thereby the syntactic structure of the jabberwocky sentence was retained, providing a proper basis to predict the word category of the target word, but not its meaning (cf. Figure 2-3). Finally, in order to discover the neural basis of syntactic prediction processes, both normal and jabberwocky sentences should be compared to a baseline condition that also includes visual word-like input but does not provide a basis for a syntactic prediction (i.e., non-word lists; NWL).

To sum up, as depicted in the lower panel of Figure 2-3, during each trial a linguistic context was established, suggesting either a specific meaningful target word (SENT), the target words' syntactic category (JAB), or neither syntactic category nor semantic content (NWL). The target word was delayed by 1.625-4.225 seconds, thereby opening up a time gap for the participants to anticipate it (i.e., prediction phase, cf. Figure 2-4). Afterwards, a target word was presented (a verb or a noun), and the participants had to decide, whether the target word was a grammatically valid continuation of the preceding word sequence (i.e., TASK). During the prediction phase, the participants were expected to display anticipatory eye movements into the grammatically valid target word area in SENT and JAB, but not in NWL.

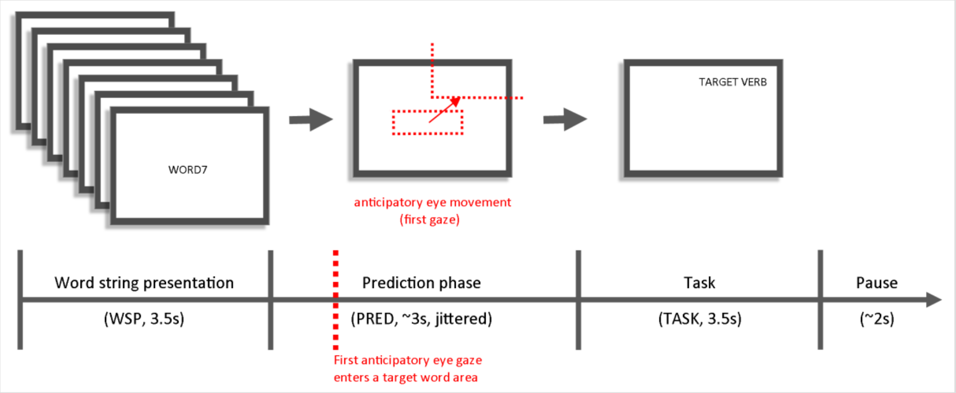


Figure 2-4: Experimental trial.

2.4.2.1 STIMULUS CREATION & PRETEST OF STIMULUS SET

To induce a prediction of a meaningful word, eight-word sentences with either a verb (e. g. “tragen”/”to carry”) or a noun (e.g. “Trage”/”barrow”) at the sentence final position (i.e., target word, cf. Figure 2-3) were created. Grammatically valid and invalid target words were not only matched on a semantic level, but also contained the same number of syllables. After establishing these word sequences for the sentence condition (SENT), content words (such as “Sanitäter”/”paramedic”) were exchanged by pronounceable non-words to acquire a meaningless jabberwocky condition (JAB) with retained syntactic structure. Due to the loss of content words, it was highly unlikely that participants would be able to predict the meaning of the target word; however, predicting the target words’ syntactic category remained possible. Finally, a pure non-word list (NWL) was created, serving as a high-level baseline that neither induced predictions of meaningful words nor syntactic categories. Note that all pronounceable non-words in JAB and NWL were created by mixing up the syllables of the original words and concatenating them in a non-meaningful way. Thus, syllable length of words and total length of word sequences was matched across all conditions, rendering effects based on amount of input unlikely.

Pretest and stimulus selection. Given that the experiment was designed to reveal the neural substrate of linguistic predictions, in a first step it was necessary to assure that the SENT conditions led to very clear predictions regarding the target word (meaning and syntactic category). Additionally, both SENT and JAB were expected to elicit strong predictions regarding the syntactic category of the target word while NWL were not. To test whether these requirements were met by the stimuli, an online questionnaire was set up for a total 44 of item sextets (i.e., verb/noun target, SENT/JAB/NWL version) using the online survey application LimeSurvey (www.limesurvey.org). Twenty native German participants (10 female, mean age = 24.4 years; age sd = 2.4) were invited to complete the following tasks:

(a) To fill in target words for sentences (in order to check whether participants have common associations regarding the target word, i.e. cloze probability[6])
(b) To specify the syntactic category of the target word (i.e., which syntactic category would the missing target word belong to) for SENT, JAB and NWL.
(c) To check non-word lists for strong spontaneous associations to meaningful words and indicate those non-word-and-word pairs.

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[6] “Cloze probability” refers to the probability that participants produce a specific word in a sentence completion task (Coulson, 2007)

The final set of 30 item sextets contained only items that had (a) a very high cloze probability (mean = 89.83, sd = 13.40) for SENT, (b) a very high syntactic probability for both SENT (mean = 99.16, sd = 1.90) and JAB (mean = 96.58, sd = 5.56), but not NWL (mean = 32.33, sd = 12.12), and (c) did not evoke strong associations of non-words to existing meaningful words.

2.4.2.2 BEHAVIORAL PILOT STUDY

Before conducting a combined fMRI and eye tracking study, it was of major interest to assure that the paradigm described above worked properly in terms of response behavior and anticipatory eye movements. Participants were expected to be very confident about the grammatical acceptability of the target word in SENT and JAB, but not in NWL, leading to a better behavioral performance in the former conditions. Specifically, it was hypothesized that responses in the two-alternative forced choice task (i.e., judging the grammatical acceptability of the target word given the preceding word sequence: "yes" vs. "no") would be slightly faster and more accurate in the context of SENT compared to JAB. In NWL the aim was to remove all cues suggesting a specific syntactic category, thus a random response pattern was expected (indicated by chance level performance).

Regarding the anticipatory eye gazes during the prediction phase, hypotheses were generated for three eye tracking parameters. The first parameter, namely the ***time until the first saccade reached a target word area*** (TWA, possible screen positions of the target words, i.e. upper/lower right corner), was operationalized as the time it takes the participants to move their eye gaze from the center of the screen (where the last word of the word sequence is presented, cf. Figure 2-3 and 2-4) to one of the TWAs.

$$\begin{aligned} &time\ until\ the\ first\ saccade\ reached\ a\ target\ word\ area\ (in\ msec) \\ &\qquad = time\ point\ when\ the\ eye\ gaze\ enters\ the\ TWA \\ &\qquad - start\ of\ 7th\ word\ of\ the\ previous\ word\ string \end{aligned}$$

The time parameter was taken as an indicator for the confidence and ease of the anticipation: If the participants were very confident about the target word category they expect, then they were hypothesized to shift their eye gaze to the respective corner very fast (and vice versa). This hypothesis already implies a second parameter, namely ***accuracy of the first gaze*** (i.e., the percentage of anticipatory first gazes into the grammatically valid TWA). This accuracy was hypothesized to be higher in conditions that allowed to predict the grammatical category of the target word (i.e., SENT and JAB) than in the condition that did not encourage a prediction (i.e., NWL). More specifically, since participants should not be able to build up a specific syntactic prediction in NWL, it was hypothesized that in NWL the first gaze were shifted randomly to one or the other target word area, resulting in 50% chance for both TWAs to be fixated first.

$$Accuracy\ of\ first\ gaze\ (in\ \%)$$
$$= \frac{1st\ gazes\ into\ valid\ TWA}{(1st\ gazes\ into\ valid\ TWA + 1st\ gazes\ into\ invalid\ TWA)} * 100.$$

Independent of whether or not participants shifted their eye gaze to the grammatically valid TWA first, the question remained whether they would stick with their first choice over the whole prediction phase or fixate both TWAs. Therefore, the third dependent measure investigated here was the ***valid anticipatory fixation time***, which is the percentage of the anticipatory fixation time spent in the grammatically valid target word area compared to the overall time spent in both target word areas:

$$\%\ fixation\ time = \frac{fixation\ time\ of\ predictable\ TWA}{(fixation\ time\ of\ predictable\ TWA + fixation\ time\ of\ other\ TWA)} * 100.$$

It was hypothesized that participants would fixate the grammatically valid TWA more extensively in conditions that allow for a clear grammatical decision regarding the expected target word (i.e., normal and jabberwocky sentences). In contrast, when presented with non-word lists, it was assumed that the participants should not be able to make a clear prediction and therefore spend equal amounts of time fixating both TWAs.

Experimental procedure. Eighteen German natives without a history of language disorders or other mental illnesses (9 female; mean age = 25.2; sd age = 2.8) were instructed and tested in accordance with the Declaration of Helsinki (2008, World Medical Association, www.wma.net/en/30publications/10policies/b3) using the Tobii X2-60 eye tracking system described in section 2.2. During the whole experiment, participants were comfortably seated in front of the eye tracking system in a computer laboratory. Participants were familiarized with the task via verbal and written instructions as well as a short training procedure (24 Trials). This training procedure was necessary to establish a strong association between grammatical category and screen position of the target words. To establish this association, participants were first presented with eight normal and jabberwocky sentences ending with a verb in the upper corner first, then eight sentences with the respective items counterparts ending with a noun, followed by a mixed set of normal sentence, jabberwocky sentences and non-word lists. Note, however, that the screen position of the categories were not explicitly mentioned in the instruction and thus only could be implicitly learned by the participant. After task completion, all participants were compensated with 7 EUR per hour.

Analysis and results I: Response times and accuracy. One participant had to be excluded from the behavioral analysis for technical reasons (i.e., button presses were not recorded). For the remaining 17 participants a general linear model was set up (GLM, repeated measures) estimating the impact of the within-subject factor STRUCTURE (levels: SENT, JAB, NWL) on response times and accuracy. Results for both dependent measures are detailed in Table 2-1.

Because for both response times and accuracy the main effect of STRUCTURE reached statistical significance, post hoc tests (i.e., paired t-tests) were estimated. As depicted in Figure 2-5A, responses to target words in a sentence context were given faster compared to jabberwocky items (t(16) = 8.51, p < .001) and non-word lists (t(16) = 11.31, p < .001). In line with the hypotheses, jabberwocky items led to faster responses than non-word lists (t(16) = 6.25, p < .001) as well.

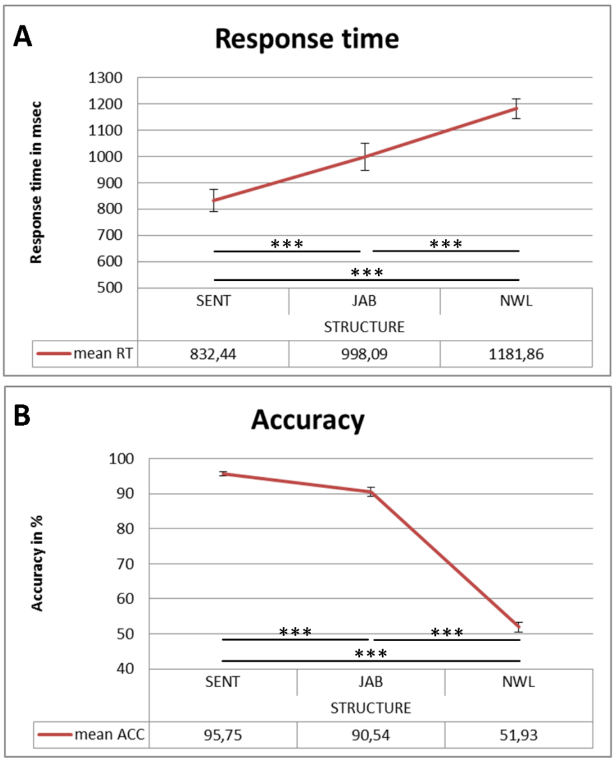


*Figure 2-5: Behavioral performance. Results of post-hoc comparisons (paired t-tests, Bonferroni corrected). SENT, normal sentences; JAB, jabberwocky sentences; NWL, non-word lists; RT, response time; ACC, accuracy; ***, p < .001.*

Table 2-1: Behavioral performance. Results of the general linear models (repeated measures) calculating the impact of the within-subjects factor STRUCTURE (normal sentences (SENT) vs. jabberwocky sentences (JAB) vs. non-word lists (NWL)) for response times and accuracy. F, test value for GLM; p, probability for null-hypothesis to be accepted; partial η2 , effect size measure; df, degrees of freedom; (*), because the criterion of sphericity was violated, a Greenhouse-Geisser correction was applied.

Dependent measure	F	df	p	partial η^2
Response times	69.159	2	.000	.902
Accuracy	635,476	1,265(*)	.000	.988

A different picture emerged when the impact of STRUCTURE on the ***accuracy*** of responses was estimated (cf. Figure 2-5B). In line with the hypotheses, post-hoc tests showed that accuracy of responses was very high in both normal and jabberwocky sentences while it was at chance level for non-word lists (t(16) = 1.41, p = .179). Contrasted directly, responses were more accurate for normal compared to jabberwocky sentences (t(16) = 6.58, p < .001) and to non-word lists (t(16) = 32.87, p < .001). Jabberwocky sentences also led to increased accuracy rates than non-word lists (t(16) = 22.27, p < .001).

Analysis and results II: Eye tracking. For all three eye tracking parameters a general linear model (repeated-measures) was estimated including the within-subject factor STRUCTURE (levels SENT, JAB, NWL, cf. Table 2-2). Results reveal a significant main effect of STRUCTURE for the percentage of fixation time of the predictable target word area (TWA) as well as the percentage of first eye gazes into the predictable TWA.

Table 2-2: Anticipatory eye movements. Results of the general linear models (repeated measures) calculating the impact of within-subjects factor STRUCTURE (normal sentences (SENT) vs. jabberwocky sentences (JAB) vs. non-word lists (NWL)) for all eye tracking parameters. F, test value for GLM; p, probability for null-hypothesis to be accepted; partial η2 , effect size measure; df, degrees of freedom; (*), because the criterion of sphericity was violated, a Greenhouse-Geisser correction was applied.

Dependent measure	F	df	p	partial η2
Saccade duration of first gaze (in msec)	23.391	2	.000	.594
Accuracy of first gaze (in %)	8.482	1.327(*)	.005	.346
Valid anticipatory fixation time TWA (in %)	9.260	1.339(*)	.003	.367

Starting with the first eye tracking parameter, the ***saccade duration*** (i.e., the time it took the participants to shift their eye gaze from the center of the screen to one of the possible target word area) pointed towards predictive eye movements for sentences and jabberwocky (cf. Figure 2-6A). Post-hoc paired t-tests revealed that saccade duration was significantly reduced for sentences as compared to jabberwocky (t(16) = 4.61, p < .001) and non-word lists (t(16) = 6.04, p < .001). In line with the hypotheses, jabberwocky sentences also led to significantly faster anticipatory saccades into the target regions than non-word lists (t(16) = 2.522, p = .023).

A slightly different result pattern emerged from the ***accuracy of the first gaze***, (i.e., the percentage of first gazes into the grammatically valid target word area; cf. Figure 2-6B). The accuracy of the first gaze did not differ between normal and jabberwocky sentences (t(16) = 0.63, p = .536); however both normal sentences (t(16) = 3.24, p = .005) and jabberwocky sentences (t(16) = 2.87, p = .011) led to significantly enhanced first gaze accuracy compared to non-word lists. Notably, in both normal (t(16) = 3.08, p = .007) and jabberwocky sentences (t(16) = 2.67, p = .017) the accuracy

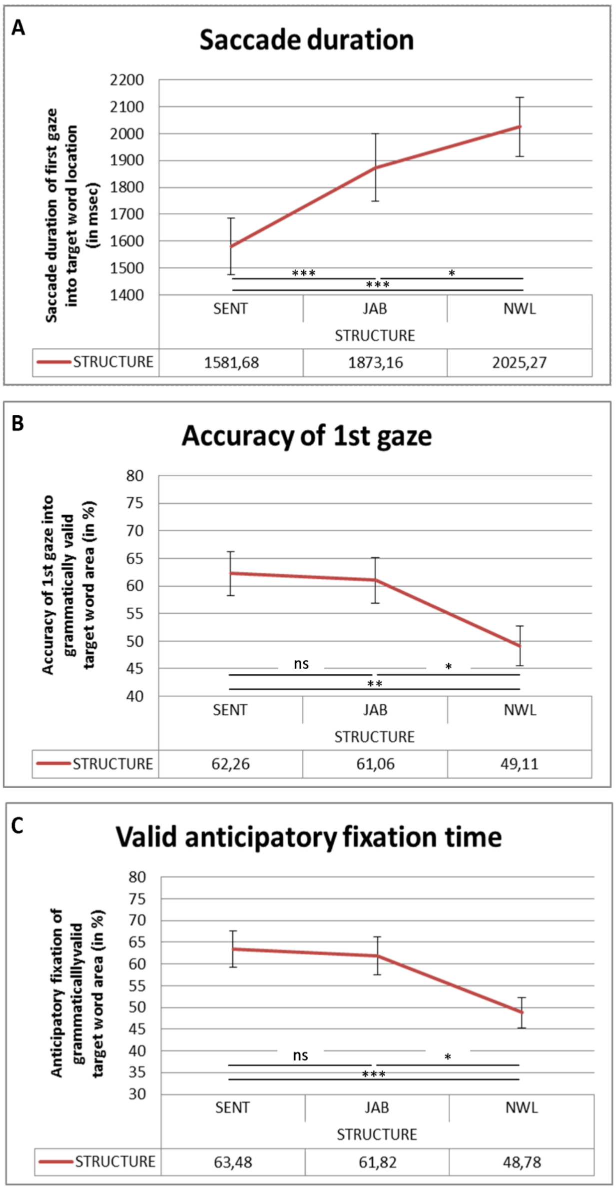


*Figure 2-6: Eye tracking performance in terms of saccade duration, accuracy of first gaze and the percentage of valid anticipatory fixation. SENT, normal sentences; JAB, jabberwocky sentences; NWL, non-word lists; ns, not significant; *, p < .05; **, p < .01, ***, p < .001.*

was significantly above chance level; the opposite was true for non-word lists (t(16) = 0.25, p = .806).

Although participants preferentially moved their eyes into the grammatically valid target word area first, chances remain that they shift their eye gaze over the course of the prediction phase if they are not certain about the word category they should expect. Therefore, a third parameter was investigated, namely the percentage of the fixation time spent in the grammatically valid target word area compared to the overall time spent in both target word areas (TWA).

In normal and jabberwocky sentences, the valid TWA was determined by the preceding word sequence (e.g. if a verb was expected as a target word, its position on the screen was predictable). Post-hoc tests demonstrated that there was no significant difference between normal and jabberwocky sentences with respect to the percentage of valid anticipatory fixation (t(16) = 0.81, p = .431). However, compared to non-word lists, in both normal (t(16) = 3.35, p = .004) and jabberwocky sentences (t(16) = 3.03, p = .008) participants fixated the grammatically valid target word area prior to target word presentation more extensively (cf. Figure 2-6C). In line with the hypothesis, in case of non-word lists participants randomly fixated both target regions (i.e., fixation time for both areas was not different from chance level; t(16) = 0.35, p = .731) while they showed a significant preference for the grammatically valid target region in both normal (t(16) = 3.24, p = .005) and jabberwocky sentences (t(16) = 2.68, p = .016).

Discussion and outlook. The pilot study of the syntactic prediction project aimed at testing whether or not the present eye tracking paradigm is useful to demonstrate the existence of linguistic predictions based on syntactic structure with anticipatory eye gazes. Within the context of (a) normal sentences (i.e., with intact syntactic structure and semantic context) and (b) jabberwocky sentences (i.e., items with function words that preserve the syntactic structure, but without content words which are exchanged with pronounceable non-words) it was hypothesized that participants should automatically make a prediction about the word category of the sentence final word. In contrast, given (c) a pure non-word list, participants should not be able to predict the target word category. Response times and accuracy of responses supported this assumption: response times for normal and jabberwocky items were fast and accurate, whereas when participants were presented with non-word lists, they responded slowly and displayed a random response pattern.

However, since the major purpose of creating the present paradigm was to measure the predictive process using eye tracking, the most important question was whether or not participants would display anticipatory eye gazes. Since the target word category was associated to a specific position on the screen and the presentation of the target word itself was delayed, participants had time to shift their eye gaze according to their prediction of the target word category *before* actual target presentation, given that they engaged in linguistic prediction in the first place. Indeed, the eye tracking data demonstrated that participants not only relocated their eye gaze into the target word areas more quickly in the context of SENT and JAB compared to NWL. Moreover, they also shifted their gaze into the grammatically acceptable target word area more often than into the unacceptable one. Notably, neither the association between target word area and grammatical category nor the prediction itself was part of the instruction. The aforementioned results thus demonstrate two effects. First, according to the eye tracking data, participants learned the association between target word category and its respective location on the screen without explicit instruction. Second, although the task did not necessarily ask for predictive processing (i.e., participants could have waited for the final target word and then evaluate the grammatical acceptability without predicting the target word category beforehand), participants showed a preferences to shift their eye gaze into the grammatically acceptable target word area significantly more often and fixated this regions longer in conditions providing syntactic structure (i.e., normal and jabberwocky sentences) than in the context of non-word lists. This might be taken as a clear hint towards predictive processing based on syntactic structure. Therefore, the paradigm is well suited to investigate the neural substrates of linguistic predictions in the magnetic resonance (MR) scanner. However, because in sentences and jabberwocky the ratio between accurate and inaccurate anticipatory eye gazes was only about 2:1, a couple of changes to the experimental paradigms were introduced before conducting the experiment in the MR scanner.

The following list provides an overview of all adaptations applied to the paradigm prior to the fMRI measurement:

1. To lead participants to more rapid predictive eye movements in general, the salience of the possible word locations on the screen should be enhanced. Therefore, three light grey boxes were shown throughout each experimental trial (cf. Figure 2-7), indicating (a) the position of the context word sequence in the middle of the screen, (b) the first target word area in the upper right corner of the screen and (c) the second target word area in the lower right corner of the screen. By this, participants' eye gaze should be drawn more rapidly into one of the target word areas during the prediction phase.

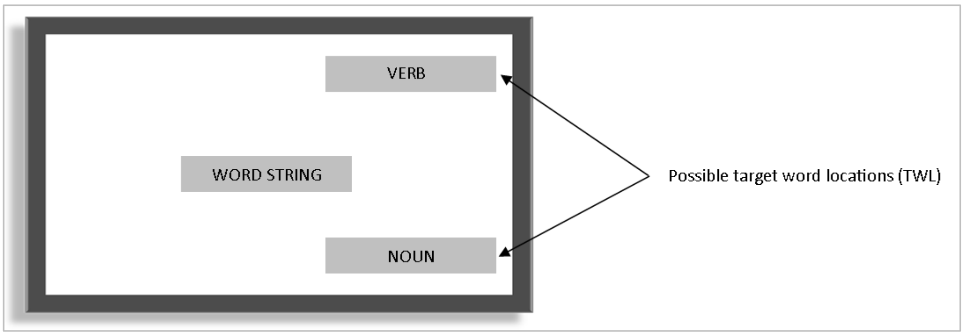


Figure 2-7: Screen positions of words highlighted by grey boxes.

2. To be absolutely certain that participants learned the association between target word category and its respective location on the screen, I decided to include this association in the instruction (i.e., participants were instructed that a verb target would always be presented in the upper right corner, while a noun target would always appear in the lower right corner). However, no instructions regarding an anticipatory eye movement were given, since the predictive process was not supposed to be explicitly forced by the instruction.
3. According to the saccade duration, it takes participants approximately 1.5 seconds to shift their eye gaze from the center of the screen into the target word region in the fastest (i.e., sentence) condition, and even longer in the other conditions. Due to our jitter in some of the trials the duration of the prediction phase was only 2.125 seconds; thus it is possible that the present paradigm missed valid eye gazes. Therefore, in the fMRI experiment, the prediction phase was prolonged to a minimum of 3.5 seconds.
4. After the experiment, some participants mentioned that over the course of the experiment they recognized some of the normal sentences when their jabberwocky counterparts were displayed, leading to semantic context not only in the normal sentences, but also in the jabberwocky sentences. For this reason, the item list was split in part A and part B (matched for syllable length and cloze probability), giving half of the fMRI participants sentences A, jabberwocky B and non-word lists B and the other half of the group sentences B, jabberwocky A and non-word lists A (cf. chapter 4 and appendix 6.1.2).

2.4.3 PROJECT 3: PREDICTING WORDS AND SEMANTIC CATEGORIES

After the promising results of the syntactic prediction project, namely the inevitable uninstructed prediction of syntactic categories, one obvious question remained: What about a purely semantic prediction? Which brain systems support semantic predictions? And how does as purely semantic prediction compare to a combined syntactic-semantic prediction of a meaningful word? To pursue this question, the syntactic prediction paradigm described in section 2.4.2 was adapted in order to elicit semantic predictions.

2.4.3.1 STIMULUS CREATION AND PRETEST OF STIMULUS SET

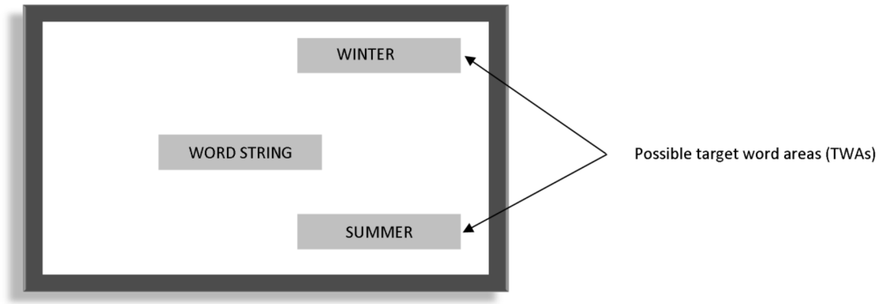
To shed light on the neural substrates of semantic predictions, a linguistic context was established, but instead of suggesting a certain syntactic category (i.e. verb vs. noun) for the last word of a word sequence, a specific *semantic* category was highly probable (cf. Figure 2-8); in our case summertime (e.g. "flip-flops") or wintertime (e.g. "Christmas tree"). Because the paradigm adaption required a completely new stimulus set, in a first step 156 eight-word sentences (76 summer sentences, 80 winter sentences) were created, containing either winter- or summer associations (cf. Figure 2-8). Afterwards, a pure semantic condition lacking sentence structure was generated by maintaining all content words (e.g. "Christmas tree") but mixing up the syllables of all other words and re-grouping them into non-words without a meaning (cf. Figure 2-8). Finally, in order to produce a condition that did not provide any cues regarding syntax or semantics, all syllables of the original sentence were mixed up and re-grouped into meaningless non-words lists.

Thirteen German natives (seven female, mean age = 25.8, age sd = 2.4) completed the stimulus pre-test using an online survey based on the open-source tool LimeSurvey (Version 1.9, www.limesurvey.org). Participants indicated with a slider on a scale from 0 (i.e., definitely summer target) to 100 (i.e., definitely winter target) to which semantic category they believed the target word should belong to. In addition, for sentences the cloze probability for a specific word was assessed. The desired final stimulus set was intended to consist of items that

(a) had a very high cloze probability in the normal sentence version,
(b) a high semantic probability (i.e., the probability to belong to the semantically correct domain in the pure semantics condition), and
(c) an indecisive response pattern (i.e., values around 50) indicating no preference for winter or summer target words in the non-word lists.

The final set of 60 item-triples (listed in appendix 6.1.3) comprised items with a mean cloze probability of 95.6 percent (sd = 5.9) in the normal sentence version, a very high semantic probability in the pure semantic condition (mean = 88.2, sd = 3.8), and no preference for winter or summer in non-word lists (mean = 49.1, sd = 3.3). The stimulus material test was thus successfully completed; however, before investigating the brain structures supporting semantic predictions, the adapted paradigm was piloted in a behavioral eye tracking study.

2.4.3.2 BEHAVIORAL STUDY



Condition	(Non-)word string	Target word (winter/summer)
SENT	Am | Himmel | über | dem | Freibad | scheint | die *In the | sky | over | the | open air bath | shines | the*	Sauna *sauna*
SEM	Üd | Himmel | amschei | emb | Freibad | tiend | re	vs.
NWL	Üd | Freimel | amschei | emb | Himbad | tiend | re	Sonne *sun*

Figure 2-8: Association of screen location and semantic category of the target word, experimental conditions and item examples. SENT, normal sentences; SEM, semantics; NWL, non-word lists.

Similar to the first prediction project, in the second prediction project we were again eager to find online eye tracking evidence for the existence and timing of linguistic predictions. However, this time the experiment focused on semantic rather than syntactic prediction processes.

The rational of the semantic prediction paradigm was as follows: Participants were first presented with a sequence of seven (non-)words, establishing a semantic context (i.e., summer or winter) in normal sentences and the pure semantic condition, but not in the non-word lists. The eighth, final (i.e. target) word was delayed by 1.6-2.4 seconds, and presented in the target area specific for the respective semantic category (e.g., summer target words in the upper right corner, winter target words in the lower right corner). During the delay, that is before the actual target word was presented, we measured anticipatory eye gazes into the target areas. We hypothesized that participants would shift their eye gaze quickly into the semantically matching target word region and fixate it in the sentences and the pure semantic condition because they predicted that the target word should belong to this category. However, in the context of non-word lists without any semantic cues, a prediction of the semantic category of the target word should be impossible; therefore participants were expected to display slower, random eye movements into both target regions.

The speed of the first eye gaze into one of the target areas was again operationalized as the ***time until the first saccade reached a target word area***. The duration was estimated by measuring the time it takes the participants to shift their eye gaze from the center of the screen (position of the word sequence elements, cf. Figure 2-8) to one of the TWAs:

$$\begin{aligned}
&time\ until\ the\ first\ saccade\ reached\ a\ target\ word\ area\ (in\ msec)\\
&\qquad = time\ point\ when\ the\ eye\ gaze\ enters\ the\ TWA\\
&\qquad - start\ of\ 7th\ word\ of\ the\ previous\ word\ string.
\end{aligned}$$

As described above, the time until the first saccade reached a target word area was taken as the first indicator for a predictive process. More specifically, it was expected to mirror the confidence of the prediction, because a strong prediction was hypothesized to results in a quick and firm anticipatory eye movement. If the eye movement indeed was anticipatory in nature, participants should not randomly redirect their eye into one of the target word areas, but rather fixate the semantically expectable target word region. Thus, the ***accuracy of the first gaze*** (i.e., the percentage of anticipatory first gazes into the grammatically valid TWA) was assumed to be high in conditions that allowed predicting the grammatical category of the target word (i.e., SENT and JAB). In contrast, NWL should not provide any cues triggering semantic predictions, thus the first gaze should be shifted randomly to one or the other target region, resulting in 50% chance for both TWA to be fixated first in the NWL condition.

$$Accuracy\ of\ first\ gaze\ (in\ \%) = \frac{1st\ gazes\ into\ valid\ TWA}{(1st\ gazes\ into\ valid\ TWA + 1st\ gazes\ into\ invalid\ \ TWA)} * 100.$$

However, anticipatory first gazes are only the first part of the eye tracking hypotheses – additionally, it was assumed that the participants would also stick to their decision regarding the expected target word category (i.e., spend more time fixating the respective target word area over the course of the prediction phase). Therefore, we estimate the ***valid anticipatory fixation time*** by estimating the percentage of the anticipatory fixation time spent in the semantically valid target word area compared to the overall time spent in both target word areas:

$$\% \, fixation\ time = \frac{fixation\ time\ of\ predictable\ TWA}{(fixation\ time\ of\ predictable\ TWA + fixation\ time\ of\ invalid\ TWA)} * 100$$

We hypothesized that participants fixate the semantically valid TWA more extensively in conditions that allow for a clear semantic decision regarding the expected target word (i.e., in sentences and pure semantics). In contrast, when presented with non-word lists, we assumed that the participants should not be able to generate a prediction and therefore spend equal amounts of time fixating both TWAs.

Although eliciting and measuring anticipatory eye movements was the major focus of the paradigm developed here, it was also necessary to assure that sentences and pure semantic conditions lead to a high accuracy in the semantic judgment task (i.e. to rate whether the target word was semantically valid given the preceding word sequence). In contrast, non-word lists should not establish a preference for any semantic category, hypothetically resulting in slower, more hesitant responses with a random response pattern. To evaluate these assumptions, response time and accuracy were obtained additionally.

Experimental procedure. Twenty-four German native participants were invited for the behavioral pilot study. One female participant had to be excluded for technical reasons (i.e., eye tracking data loss), the remaining group (right-handed according to the Edinburgh handedness test, 11 female, mean age = 28.4, age sd = 2.5) completed the experiment and was financially compensated with 7 EUR per hour. Each participant received extensive information and was instructed and treated according to the guidelines of the World Medical Association (Declaration of Helsinki, Version of 2008, www.wma.net/en/30publications/10policies/b3/). During the whole experiment, participants were comfortable seated in front of the Tobii T120 eye tracking system (see chapter 2.2 for a detailed description of the eye tracking methodology). Their task was to rate whether or not the target word represented a semantically correct (i.e., winter or summer) continuation of the preceding word sequence. Note that the target word always matched the preceding word sequence with respect to syntax (e.g., if a verb was missing at the final position, a semantically matched or not matched target verb was presented). Participants responded to each item via button press with their left and right thumb, indicating a “yes” or “no” answer. Button assignment was counterbalanced across participants. After listening to the instructions, participants underwent a training procedure in order to become familiarized with the task and, most importantly, with the assignment of winter and summer target words to the upper and lower right corner of the screen, respectively. Again, winter and summer assignment to screen positions were counterbalanced across participants, but remained constant for each participant during the whole experiment to ensure a secure association between semantic category and screen position as a basis for anticipatory eye movements.

Analysis and results I: Response times and accuracy. A general linear model was estimated (GLM, repeated measures) to investigate the impact of the within-subject factor STRUCTURE (levels: SENT, SEM, NWL) on response times and accuracy. The significant main effects for both dependent measures are summarized in Table 2-3. Both response time and accuracy were dependent on the STRUCTURE, thus post hoc tests (i.e., paired t-tests) were estimated. In line with the hypotheses, responses to target words in a sentence context were given faster compared to semantic items (t(22) = 3.61, p = .002) and non-word lists (t(22) = 5.45, p < .001). Furthermore, purely semantic items led to faster responses than non-word lists as well (t(22) = 3.87, p = .001).

In terms of accuracy (cf. Figure 2-9, lower panel), participants more accurately judged the semantic suitability of the target words in the context of normal sentences than in the context of purely semantic items (t(22) = 2.70, p = .013) or in non-word lists (t(22) = 23.29, p < .001). Purely semantic items led to higher accuracy rates than non-word lists as well (t(22) = 14.66, p < .001). However, in contrast to our hypotheses, performance in non-word lists was slightly above chance level (t(22) = 5.37, p < .001), indicating that most, but not all cues regarding the semantic category were deleted from the non-word lists.

Table 2-3: Results of GLM (repeated measures) for behavioral measures investigating the

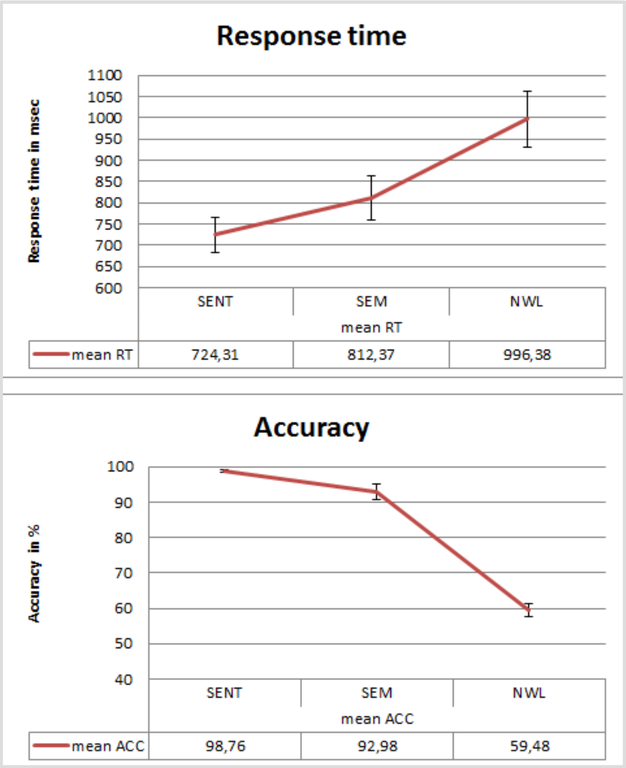


*Figure 2-9: Behavioral performance. Results of post-hoc comparisons (paired t-tests, Bonferroni corrected). SENT, normal sentences; SEM, semantics; NWL, non-word lists; ***, p < .001; **, p < .01; *, p < .05.*

within-subjects factor STRUCTURE. F, test value for GLM; p, probability for null-hypothesis to be accepted; partial η2 , effect size measure; df, degrees of freedom; (*), because the sphericity criterion for GLM was violated according to Mauchly's test of sphericity, a Greenhouse-Geisser correction was applied.

Dependent measure	F	df	p	partial η^2
Response time (in msec)	21.634	1.381(*)	< .001	.618
Accuracy (in %)	213.336	2	< .001	.907

Analyses and results II: Eye tracking. For four subjects, we were not able to estimate predictive eye movements; results from the pilot study of syntactic prediction project indicated that for some participants, the length of the prediction phase (1.6 seconds) might not have been sufficient to shift their eyes into the target word areas. For this reason, those participants were excluded from the eye tracking analyses. For the remaining group of 19 participants, a general linear model (repeated-measures) estimating the impact of the within-subject factor STRUCTURE (levels SENT, SEM, NWL) was generated for each of the three eye tracking parameters. The main effect of STRUCTURE reached significance for all three parameters; results are summarized in Table 2-4.

Table 2-4: Anticipatory eye movements. Results of general linear model (repeated measures) estimating the impact of within-subjects factor STRUCTURE (normal sentences (SENT) vs. purely semantic items (SEM) vs. non-word lists (NWL)) for all eye tracking parameters. (*), because the sphericity criterion for GLM was violated according to Mauchly's test of sphericity, a Greenhouse-Geisser correction was applied.

Dependent measure	F	df	p	partial η^2
Saccade duration of first gaze (in msec)	29.176	2	< .001	.618
Accuracy of first gaze (in %)	36.397	2	< .001	.669
Valid anticipatory fixation time TWA (in %)	59.236	1,305$^{(*)}$	< .001	.767

First hints towards predictive eye movements in sentences and pure semantics are revealed by the ***saccade duration*** (i.e., the time it took the participant to shift their eye gaze from the center of the screen to one of the possible target word areas, cf. Figure 2-10A). Post-hoc paired t-tests confirmed that saccade duration did not significantly differ for sentences as compared to pure semantics (t(18) = 1.42, p = .173). However, in line with the hypotheses, both sentences (t(18) = 6.05, p < .001) and pure semantics (t(18) = 5.62, p < .001) led to faster saccades into the target word areas than non-word lists.

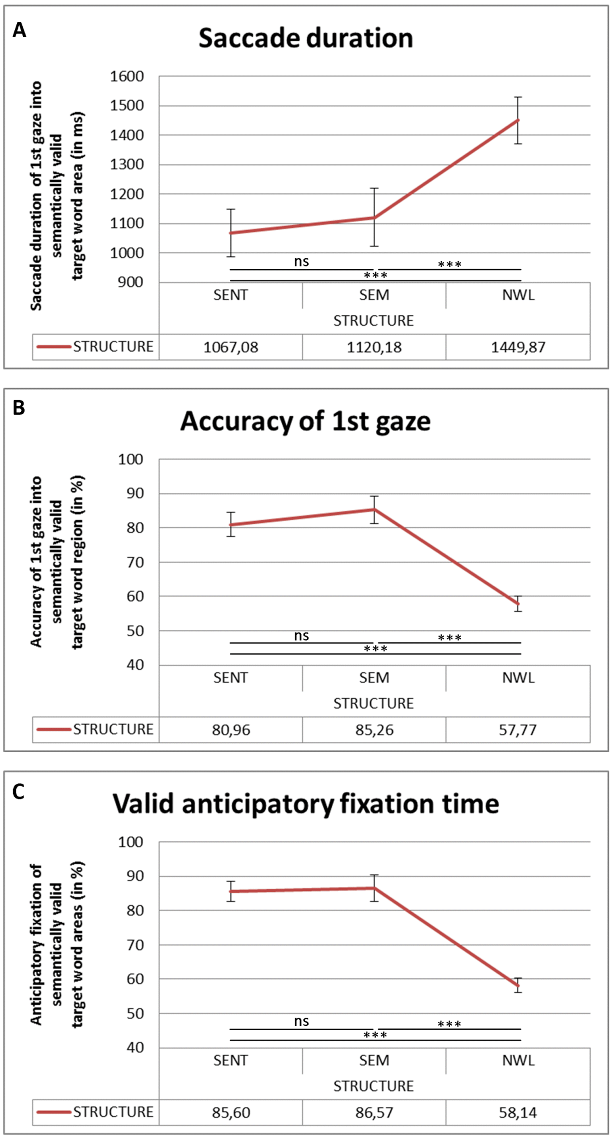


*Figure 2-10: Eye tracking performance in terms of saccade duration, accuracy of first gaze and the percentage of valid anticipatory fixation. SENT, normal sentences; SEM, semantics; NWL, non-word lists; ns, not significant; ***, p < .001.*

Although the saccade duration provides a first evidence for the existence of predictive processes, a semantic category prediction was also hypothesized to result in more accurate eye movements. To test this hypothesis, we estimated the ***accuracy of the first gaze***, (i.e., the percentage of first gazes into the semantically valid target word area; cf. Figure 2-10B). The accuracy of the first gaze did not differ between sentences and pure semantics (t(18) = 1.28, p = .217); this result was not surprising, since a prediction of the semantic category was possible in both conditions. Still, when compared to a non-word lists, both sentences (t(18) = 8.12, p < .001) and pure semantics (t(18) = 6.74, p < .001) led to significantly increased accuracy rates regarding the chosen target word area. Because we did not expect participants to generate valid predictions about the semantic category in the context of non-word lists, we hypothesized random eye movements into both target word areas. Conversely, the accuracy of the first gaze significantly differed from chance level (t(18) = 3.48, p = .003), indicating that some participants were cued regarding the semantic categories in the non-word lists as well.

The last eye tracking parameter of interest was the ***percentage of the fixation time spent in the semantically valid target word area*** compared to the overall time spent in both target word areas (TWA). Although participants preferentially shifted their eye gaze into the semantically valid target word area, chances remained that they switched between both TWAs over the course of the prediction phase if they were not certain about the semantic category they should expect. As described above, in the context of sentences and pure semantics, the valid TWA was determined by the preceding word sequence (e.g. if a winter word was expected as a target word, its position on the screen was predictable). With respect to the percentage of anticipatory fixation of the semantically valid TWA, post-hoc tests showed that participants did not spent significantly different amounts of time fixating the semantically valid TWA based on sentences and pure semantics (t(18) = 0.44, p = .667). As hypothesized, both sentences (t(18) = 10.97, p < .001) and pure semantics (t(18) = 7.30, p < .001) led to more valid fixation time compared to non-word lists, providing further indication for predictive processes prior to the actual target word presentation (cf. Figure 2-10C). However, contrary to our hypothesis, participants were not randomly fixating both target TWAs in the context of non-word lists semantics (t(18) = 3.78, p = .001). The implications of this result are discussed in section 5.2.2.

In summary, the present chapter provides an overview over the methods used and the paradigms generated and piloted over the course of the present PhD project. Building on this background, the next chapters (i.e., manuscripts) will pursue with the investigation of the neural substrate of memorizing and predicting language.

3 BRAIN SIGNATURE OF WORKING MEMORY FOR SENTENCE STRUCTURE: ENRICHED ENCODING AND FACILITATED MAINTENANCE (MANUSCRIPT I)[7]

Corinna E. Bonhage [1,5], Christian J. Fiebach [2,3], Jörg Bahlmann [4], and Jutta L. Mueller[1,5]

3.1 ABSTRACT

Sentences are easier to memorize than ungrammatical word strings, a phenomenon known as the sentence superiority effect. Yet, it is unclear how higher-order linguistic information facilitates verbal working memory and how this is implemented in the neural system. The goal of the current fMRI study was to specify the brain mechanisms underlying the sentence superiority effect during encoding and during maintenance in working memory by manipulating syntactic structure and working memory load. The encoding of sentence material, as compared with the encoding of ungrammatical word strings, recruited not only inferior frontal (BA 47) and anterior temporal language-related areas but also the medial-temporal lobe, which is not classically reported for language tasks. During maintenance, it was sentence structure as contrasted with ungrammatical word strings that led to activation decrease in Broca's area, SMA, and parietal regions. Furthermore, in Broca's area, an interaction effect revealed a load effect for ungrammatical word strings but not for sentences. The sentence superiority effect, thus, is neurally reflected in a twofold pattern, consisting of increased activation in classical language as well as memory areas during the encoding phase and decreased maintenance-related activation. This pattern reflects how chunking, based on sentential syntactic and semantic information, alleviates rehearsal demands and thus leads to improved working memory performance.

3.2 INTRODUCTION

Language and working memory are deeply intertwined. Language comprehension requires linguistic processing as well as working memory resources as soon as it gets beyond the level of single words (Caplan & Waters, 1999; Fiebach, Schlesewsky, Lohmann, von Cramon, &

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[7] This chapter corresponds to: Bonhage, C. E., Fiebach, C. J., Bahlmann, J., & Mueller, J. L. (2014). Brain Signature of Working Memory for Sentence Structure: Enriched Encoding and Facilitated Maintenance. *Journal of Cognitive Neuroscience, 26*(8), 1654-1671. doi: 10.1162/jocn_a_00566.

Friederici, 2005; Grodzinsky & Santi, 2008; Rogalsky & Hickok, 2010). In turn, structured language is known to aid working memory, which supports the assumption of a tight interaction between these two fundamental cognitive systems. An important empirical demonstration of the close relationship between language and working memory is the sentence superiority effect (SSE), that is, the observation that sentences are remembered better than ungrammatical word strings (Brener, 1940; Jefferies et al., 2004; Perham et al., 2009). Interestingly, the SSE is not restricted to full sentences but also holds true for small fragments, for example, word pairs. Perham et al. (2009) used adjective– noun pairs either in the correct or reversed grammatical order, observing a superior recall for items with a grammatically correct word order. The present article tackles the question how the SSE unfolds over the first consecutive stages of the memorizing process (i.e., encoding and maintenance) and how it is neurally implemented. In addressing the question why memorizing sentences in verbal working memory is facilitated, Baddeley, Hitch, and Allen (2009) argue that the—phonologically coded— linguistic material interacts with knowledge about the sequential redundancy in language to bind chunks of multiple items. The importance of sequential redundancy was already highlighted decades earlier when Miller and Selfridge (1950) conducted a study where they gradually increased the dependent probability of words in word strings (i.e., the probability of certain words to occur after each other in natural language, which is constrained more and more over the course of a sentence). Here, it was shown that the more similar the word string was to natural language (i.e., high dependent probability), the more successful participants were in recall.

In contrast to this proposal, other authors have argued that recalling sentences is fundamentally different from recalling word lists, based on their observation that STM for word lists is carried mainly by phonological information, whereas STM for sentences relies on semantic information (Potter & Lombardi, 1990). Following up this observation, Potter and Lombardi put forward the conceptual regeneration hypothesis (CRH), stating that sentences are recalled based on their meaning, using previously utilized and thus primed words and syntactic structures (Potter & Lombardi, 1990, 1998). Note that sentence-level semantics emerges from the combination of single words and phrases via syntactic structure (the principle of compositionality, e.g. Hagoort, 2009; Pylkkanen, Oliveri, & Smart, 2009), leading to a semantically enriched overall representation. A comprehensive account of the SSE, however, should take into account that different levels of linguistic representation (phonology, syntax, and semantics) can contribute to short-term or working memory for sentences, because recent studies showed that both phonological (Schweppe, Rummer, Bormann, & Martin, 2011) and syntactic (Schweppe & Rummer, 2007) information are retained during immediate sentence recall. In turn, this result might be taken to suggest that syntactic structure conveys the sequential redundancy in language. Specifically, in sentences, the order of words belonging to specific grammatical categories is highly predictable (e.g., an adjective after a determiner is usually followed by a noun), leading to the sequential redundancy that Baddeley et al. (2009) regarded as being helpful for successful memorizing.

A more general account of the SSE may arise from process models of working memory such as the active memory model by Zhou, Ardestani, & Fuster (2007) or the embedded processing model of working memory by Cowan (1999). On the basis of these models, one would predict that verbal working memory (VWM) is a state of sustained activation in relevant representations of the language system. This implies that VWM does not rely on a specific phonological component alone (i.e., the phonological loop, a subvocal articulatory rehearsal mechanism; Baddeley & Hitch, 1974). Instead, according to these models, all available representational properties of linguistic materials such as phonology, semantics, or syntax can be kept in an activated state, which serves as the basis of the maintenance of information in VWM. In support of this, it was shown, for example, that both lexical (Fiebach et al., 2006) and word-level semantic information (Fiebach et al., 2007) improve working memory and modulate WM-related maintenance activity by recruiting language-related areas.

With respect to the underlying neural resources, it appears that the temporary maintenance or manipulation of current relevant information relies on a fronto-parietal working memory network (Curtis & D'Esposito, 2003; Rottschy et al., 2012; Salmon et al., 1996), which, however, is modulated depending on working memory contents. In a recent meta-analysis, Rottschy et al. (2012) report that both verbal WM and non-verbal WM rely on the same core network including bilateral (dorso-) lateral PFC, inferior frontal gyrus (IFG; BA 44), anterior insula, (pre-)SMA, and inferior parietal sulcus (extending into the left inferior parietal cortex). Moreover, the authors show that working memory processing of verbal material, when compared with nonverbal material, leads to increased activation within the left IFG (i.e., Broca's area; Rottschy et al., 2012). Although not all working memory studies are able to differentiate between different phases of the working memory process, there is a wide agreement in the literature that the process of memorizing can be subdivided into three stages: encoding, maintenance, and retrieval of information (e.g., Chein & Fiez, 2001). However, the neural mechanisms supporting better WM performance for sentences than for unstructured linguistic material during the different stages of the working memory process are not yet understood. Specifying these bears important implications for understanding the interaction of language and working memory in general.

Most neuroimaging studies so far have investigated the reverse question, namely, how WM supports language processing, most specifically sentence processing. During natural sentence processing, the different component processes of working memory, that is, encoding and maintenance, cannot be independently specified, because it is inherent to natural communication that maintenance of linguistic material happens simultaneously with ongoing encoding of new linguistic input. Studies investigating sentence comprehension frequently report activation of parts of Broca's area for both enhanced working memory costs (Kaan & Swaab, 2002; Rogalsky & Hickok, 2010) as well as genuine syntactic processes (Grodzinsky & Santi, 2008; Makuuchi, Bahlmann, Anwander, & Friederici, 2009), with some of the authors arguing for anatomical (but not functional) separation of the two processes (Makuuchi et al., 2009). Aside from the activation of Broca's area, these sentence processing studies frequently report anterior/ superior temporal and left IFG activation. Although these studies approach the question of how WM might assist language processing, they do however leave unanswered as to which brain areas support encoding and maintenance of sentences in WM.

This study is the first to investigate syntactic contributions to VWM in an event-related fMRI paradigm that disentangles encoding processes from maintenance processes. We studied the short-term maintenance of sentence fragments versus ungrammatical strings containing identical words to isolate the effect of sentence structure on working memory performance and brain activation patterns. We additionally manipulated working memory load (WML; items of four vs. six words in length) as well as rehearsal capacities independently. In half of the trials, phonological rehearsal was blocked using articulatory suppression (AS; i.e., participants' ongoing articulation of nonwords during the maintenance phase; Hanley & Thomas, 1984; Murray et al., 1988) thereby testing whether the SSE is affected by the availability of the phonological rehearsal system (i.e., the phonological loop as described by Baddeley's multicomponent model; cf. Baddeley & Hitch, 1974; Baddeley et al., 2009).

Previous studies in the nonlinguistic domain evidenced increased encoding-related activations for structured material (e.g., auditorily presented number sequences "8 6 4 2 3 5 7 9" vs. a random number sequence) in lateral PFC (Bor, Cumming, Scott, & Owen, 2004b; Bor et al., 2003). The latter study reported subsequently reduced maintenance-related activity in parietal and premotor cortices, leading the authors to argue that structured material allows more efficient encoding, also described as "chunking," which in turn might reduce demands in the maintenance phase (Bor et al., 2003). Given these findings, we assumed that language processing for working memory purposes leads to similar effects. As syntactic structure has a consequence for both the structural as well as the semantic representation of a sentence, we will use (in analogy to previous working memory studies including various types of memoranda), the neutral term "chunking" to describe the building of both semantic and syntactic relations during sentence encoding. Linguistically based chunking can also be described as an enriched encoding process because it entails, in addition to the simple sequence of items, semantic and syntactic relations between items. Thus, in line with Baddeley et al. (2009) who stressed the importance of binding processes during encoding of sentences and Potter and Lombardi (1998) who postulate that superior WM for sentences is strongly influenced by the generation of sentence meaning during encoding, we hypothesize that the WM benefit of sentence structure is to a large part because of enriched encoding. This enriched encoding in turn is hypothesized to result in reduced WM demands during the subsequent maintenance phase, which is compatible with the fact that Potter and Lombardi (1998) - unlike for example, process models of WM (e.g., Cowan, 1999) - assume that no specific mechanisms are additionally activated during WM for sentences.

With respect to functional neuroanatomy, we predict that enriched encoding should go along with increased activity in the fronto-temporal language network for semantic and syntactic sentence processing. Moreover, in addition to the typical language and WM-related areas (e.g., inferior/ middle frontal gyrus, inferior parietal lobule), a plausible candidate for supporting the SSE is the hippocampus. Recently, the hippocampal formation has been discussed to support binding of multiple items in working memory, also in the domain of VWM (Axmacher et al., 2010; Baddeley, Allen, & Vargha-Khadem, 2010; Sederberg et al., 2007) and, more generally, sequential pattern prediction (Buckner, 2010). It is a critical open question whether the assumed linguistic chunking during the encoding of sentence material in WM is supported exclusively by peri-sylvian language-related brain regions like Broca's area or by more domain-general memory systems like the hippocampus or whether both systems are involved in the SSE.

During the subsequent maintenance period, we expected to see reduced activity for sentence material in VWM systems responsible for phonological rehearsal because of the encoding-induced load reduction. Furthermore, the present design allows one to test the independence of the SSE from rehearsal processes during the maintenance phase. If the SSE were independent of the availability of phonological rehearsal, AS should leave working memory processing of sentence material unaffected, although at the same time, it should impair WM processing of ungrammatical strings, because the latter critically depends on the availability of the phonological loop.

3.3 METHODS

3.3.1 PARTICIPANTS

Eighteen participants (nine women, mean age = 25.0 years, range = 20–31 years) participated after giving written informed consent in accordance with the Declaration of Helsinki. Participants were compensated with EUR 8 per hour. All participants were right-handed according to their scores on the Edinburgh handedness inventory (adapted German version of Oldfield, 1971), and all were native German speakers without a known history of dyslexia, other psychiatric disorders, or neurological diseases.

3.3.2 EXPERIMENTAL DESIGN

As illustrated in Figure 1A, the present event-related fMRI working memory paradigm included the within-subject factors sentence structure (SST+ vs. SST−) and working memory load (hiWML vs. loWML), plus a third within-subject factor, articulatory suppression (AS) during maintenance (AS+ vs. AS−, separate sessions), resulting in eight conditions.

3.3.3 STIMULI

Our stimulus set comprised a basic set of 30 sentence fragments. As depicted in Figure 3-1, each set was presented as a short (four word) and a long (six word) version, and all word strings were presented with grammatical (SST+) and ungrammatical (SST−) word order, resulting in 120 items. These 120 items were presented in one session with (AS+) and one session without AS (AS−), giving a total of 240 trials. To rule out influences of word familiarity, function words were repeated across items, again limiting the overall set of words used in the present stimulus set. To keep the semantic content and associations between words as low as possible, we used sentence fragments ending within a phrase and containing mainly function words (pronouns, auxiliary verbs, and prepositions) except for temporal nouns and adverbs such as “yesterday/in the morning.” Ungrammatical word strings were generated from the sentence fragments such that each word string represented words of a specific sentence fragment in an ungrammatical word order. Thus, lexical properties, word length, and word frequency were matched between SST+ and SST−. The use of fragmentary as well as relatively content-free open-class words was intended to reduce semantic memory strategies in the ungrammatical (SST−) condition as well as possible automatic word reordering tendencies, which might be more likely if content words with their respective semantic associations were available. The material was tested in a pilot study (n = 19), resulting in matched stimulus sets with high acceptance of grammatical stimuli (SST+: mean = 99.47%, SD = 1.92%) and low acceptability ratings for ungrammatical stimuli (SST−: mean = 3.28%, SD = 9.64%). Each of the eight conditions contained 30 items, adding up to 240 items.

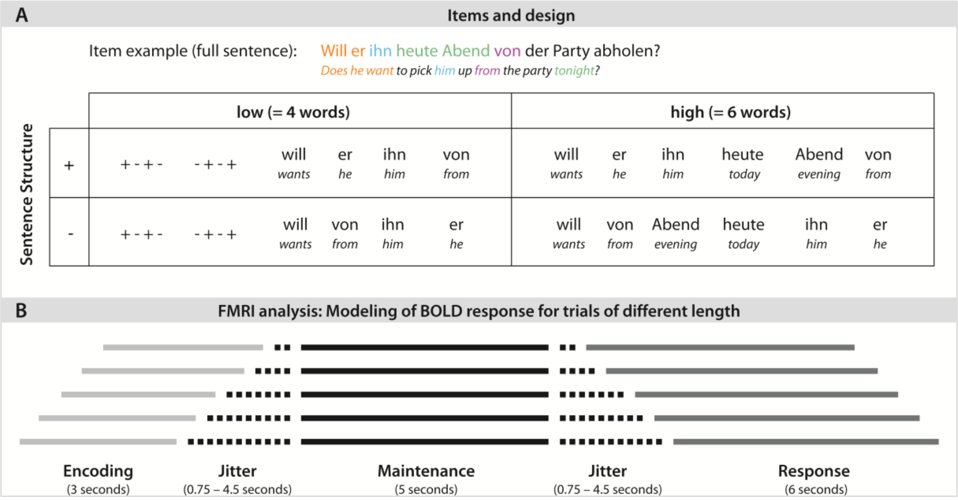


Figure 3-1: (A) Example items and design. To illustrate the construction principle for original sentence fragments, the example sentence fragment is completed to a sentence (in this case, a question) and supplemented by a translation. The colored words form the sentence fragment used in the stimulus set; the exact colors of the words indicate equivalent parts in English and German. Below this example stimulus, the design is illustrated. WML was manipulated by presenting memoranda consisting of either four words (low) or six words (high). Sentence structure was either correct (SST+) or absent (SST−), and syntactically correct sentence fragments were half-sentences with auxiliary verbs only (to assure low word-level semantics). Word-by-word English translation is given below the original items in italics. Note that the example SST+ is correct in German, although not in the word-by-word translation. Importantly, ungrammatical word strings contained the same words as sentence fragments, but in a different, ungrammatical order. All items were presented twice, once in a session with AS and once in a session without AS. (B) Modeling of BOLD responses during fMRI analysis, for encoding (light gray), maintenance (black), and retrieval (dark gray). To increase statistical independence between trial phases, a jitter before and after the maintenance phase was introduced. Jitter lengths were counterbalanced across conditions. Pauses between trials (jittered, mean = 4.75 sec) were not explicitly modeled and therefore served as implicit baseline.

3.3.4 EXPERIMENTAL PROCEDURES

During the training session and the fMRI experiment, each trial (cp. Figure 1B) consisted of four (i.e., loWML) or six (hiWML) visually presented words appearing one by one in the center of the computer screen with a rate of 0.5 sec per word (encoding). To keep visual input equal between low and hiWML conditions, four word items were preceded by strings of "+" and "–" symbols, as depicted in Figure 1A. Therefore, the total duration of the encoding period totaled 3 sec in all conditions. Participants were asked to keep the word strings in mind (maintenance period; jittered duration of 6.5, 8, 9.5, 11, 12.5, or 14 sec, jitter counterbalanced across experimental conditions). To ensure that participants would not try to "reorder" ungrammatical word strings into correct sentence structure during this delay, the subsequent task required them to remember not only word identity but also the serial order of appearance (retrieval period, duration of 6 sec). Specifically, the task was to decide whether a certain word A appeared before a certain word B (target item positions were randomized and counterbalanced across conditions). The reordering of words in ungrammatical word strings was therefore disadvantageous; none of the participants reported such a strategy. Responses were recorded using two response boxes for the left and right thumb with buttons "yes" and "no," respectively. Intertrial intervals were jittered (3.75– 4.75 sec), resulting in an average trial duration of 23.5 sec (range = 19.25–27.75 sec).

(a) Because the stimulus set was too extensive to be captured by one session and (b) to avoid task-switching related brain activation, each participant was invited for two sessions, one session with and one without AS, respectively. In the AS session, participants were instructed to lie in the scanner with the lips slightly open. During the maintenance phase of each stimulus, participants articulated a simple and meaningless German consonant–vowel syllable sequence "nenadana nenadana ..." starting with a nasal consonant and ensuring minimal jaw movement during the maintenance phase of the task. To match the rate of articulation between participants and trials, each articulation of "nenadana" was initiated by a recurring fixation cross (frequency = 1 sec) that appeared on the screen during the maintenance period. For comparability reasons, this recurring fixation cross was also shown during the maintenance in the sessions without AS. This way, in one session, it was possible to subvocally rehearse the items; the other session included AS. Order of sessions (with/without AS) was counterbalanced across participant gender and response hand assignment (yes/no button). All participants completed pre-experimental questionnaires regarding their sleep patterns and their coffee/ nicotine consumption and underwent a training procedure (30 example trials) outside the scanner before each fMRI session.

3.3.5 DATA ACQUISITION

Behavioral data were recorded using Presentation software (Version 14.1, www.neurobs.com). fMRI data were assessed using a Siemens TIM Trio 3-T scanner with continuous scanning (1,500 scans per session). A gradient echo EPI sequence was used with an echo time of 30 msec, flip angle of 90°, repetition time (TR) of 2000 msec, and an acquisition bandwidth of 116 kHz. The matrix acquired was 64 × 64 with a field of view of 19.2 cm, resulting in an in-plane resolution of 3 × 3 mm. Thirty slices were acquired with a slice thickness of 3 mm and an interslice gap of 1 mm, covering the whole brain. Before functional data, a T1-weighted 3-D magnetization prepared rapid gradient echo sequence (as described in Mugler & Brookeman, 1990) was collected for coregistration (inversion time = 650 msec, TR of the total sequence cycle = 1300 msec, TR of the gradient-echo kernel (snapshot FLASH: Haase, 1990) = 10 msec, echo time = 3.93 msec, alpha = 10°, bandwidth = 130 Hz/pixel (i.e., 67 kHz in total), image matrix = 256 × 240, field of view = 256 mm × 240 mm, slab thickness = 192 mm, 128 partitions, 95% slice resolution, sagittal orientation, spatial resolution = 1 mm × 1 mm × 1.5 mm, two acquisitions).

3.3.6 DATA ANALYSIS

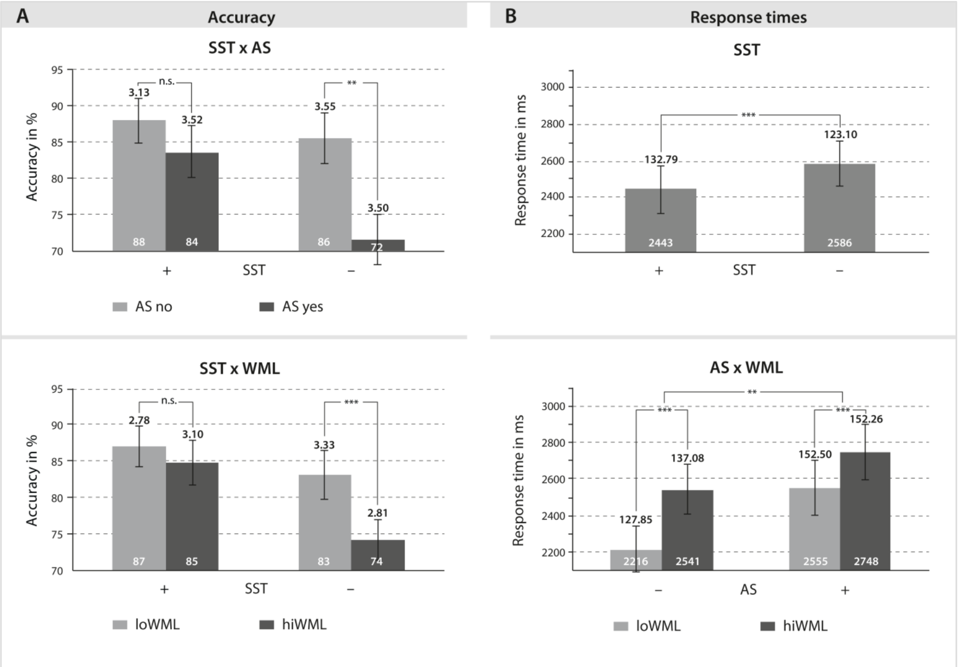
Behavioral data were analyzed using PASW Statistics 19 (SPSS, Inc., Chicago, www.spss.com), performing a repeated-measures ANOVA with three factors, that is, SST, WML, and AS, for error rates and response times (RTs) separately. All fMRI data analysis was done using SPM8 software provided by the Wellcome Department of Cognitive Neurology, London, United Kingdom. Preprocessing steps included (1) realignment to correct for head motion during scanning and coregistration of EPI images of both sessions separately to the participant's T1-weighted structural image, (2) slice timing correction with reslicing, and (3) spatial normalization into the standard stereotactic space (provided by Montreal Neurological Institute [MNI], implemented in SPM8) for group analysis. Additionally, to increase the signal-to-noise ratio, data were smoothed with an 8-mm FWHM isotropic Gaussian kernel. For first-level analysis, we modeled encoding for each condition (3 sec), an initial jitter between encoding and maintenance (0.75–4.5 sec) independent of condition, maintenance per condition (middle 5 sec of each trial, cp. Figure 1B), a jitter between maintenance and retrieval (0.75–4.5 sec) again independent of condition, retrieval per condition (full 6 sec), and button presses independent of condition, separately for both sessions. The implicit baseline included jittered pauses between trials (3.75–4.75 sec). To partial out the processes underlying error trials as well as instruction phases and half-time break, each phase was assigned to a separate regressor. Additionally, to account for head movement during scanning, realignment parameters were included in the model as well. Afterwards, to identify BOLD signal changes for each condition, second-level analysis was performed inserting first-level baseline contrast images for each condition in a flexible factorial ANOVA (2 × 2 × 2 design including the three factors SST, WML, and AS). Thereby, we directly compared effects of different conditions (e.g., with > without sentence structure, hiWML > loWML, without > with AS) and their interactions within the same model. To correct for multiple comparisons, the software package AlphaSim (Ward, 2000) performing a Monte Carlo simulation with 1,000 iterations was used. We estimated a minimal cluster size of 50 voxels, which, combined with a single-voxel threshold of $p < .001$, results in a cluster-level significance level of $p < .05$. This threshold was applied to all contrasts. For significant interaction clusters, a percent signal change analysis was performed; peak voxel values of prominent clusters were extracted per condition using the SPM toolbox MarsBar (http://marsbar.sourceforge.net), the subsequent statistical analysis (ANOVA) was performed in PASW.

3.4 RESULTS

3.4.1 BEHAVIORAL RESULTS

3.4.1.1 ACCURACY

Overall, accuracy was well above chance level in all conditions (mean values are depicted in Figure 3-2C). Participants' accuracy was higher for sentence fragments (SST+) than for ungrammatical word strings (SST−) ($F(1, 17) = 23.74$, $p < .001$), for loWML compared with hiWML ($F(1, 17) = 22.89$, $p < .001$), and when rehearsal was possible (AS−; $F(1, 17) = 6.98$, $p = .017$) compared with AS+. Additionally, sentence structure interacted with WML ($F(1, 17) = 6.51$, $p = .021$; Figure 3-2A, bottom) and AS ($F(1, 17) = 13.25$, $p = .002$; Figure 3-2A, top). Specifically, when sentence structure was available, no effects of WML or AS were evident in accuracy (both ts > −1.24). It was only in ungrammatical word strings that accuracy decreased with both AS ($t = -3.63$, $p = .002$) and hiWML ($t = -5.04$, $p = .000$). All ANOVA effects are listed in Table 1.



C **Mean values of accuracy and response times for all experimental conditions**

		– Articulatory Suppression		+	
		loWML	**hiWML**	**loWML**	**hiWML**
Sentence structure	+	88,70% 2144ms	87,40% 2423ms	85,20% 2496ms	82,20% 2711ms
	–	89,60% 2287ms	81,70% 2660ms	76,50% 2614ms	66,90% 2785ms

*Figure 3-2: Behavioral results. Facilitation effects of sentence structure were evident in both accuracies (A) and RTs (B). Accuracy: AS (A, top) and WML (A, bottom) dependent effects are visible for ungrammatical word strings (SST–) but not for sentence fragments (SST+). All main effects (AS, WM, and SST) also reached significance (not included in Figure 2). RTs: Independent of AS and WM, responses were faster for SST+ compared with responses for SST– (B, top). Differences between loWML and hiWML are significantly larger during the session without AS, compared with the session with AS (B, bottom). Both the main effects of AS and WM (not included in Figure 2) reached significance as well. (C) Mean values of RTs (blue) and accuracy (red) for all experimental conditions. Error bars represent the SEM (during maintenance phase; *p < .05, **p < .01, ***p < .001).*

3.4.1.2 RESPONSE TIMES

Mean RT values of all conditions are provided in Figure 3-2C. As shown in Table 1, participants responded faster to sentence fragments (SST+) than to ungrammatical word strings

(SST−; F(1, 17) = 36.10, p < .001), for loWML compared with hiWML (F(1, 17) = 61.40, p < .001) and when rehearsal was possible (AS−; F(1, 17) = 4.97, p = .04) compared with AS+. In addition, WML interacted with AS (F(1, 17) = 9.04, p = .008; Figure 3-2A, top), indicating that the RT differences because of AS are only significant in the loWML condition (t = 2.61, p = .018), not in the hiWML condition (t = −1.747, p = .099). Figure 3-2B illustrates the main effect of SST as well as the interaction between AS and WML.

Table 3-1: Behavioral performance. Results of general linear model (repeated measures) calculating the impact of the within-subjects factors AS (with/without), SST (+/-), and WML (low/high) for response times and accuracy. AS, Articulatory Suppression; F, test value for GLM; p, probability for null-hypothesis to be accepted; partial η2 , effect size measure; SST, sentence structure; WML, working memory load; (*).

Accuracy				**Response times**			
Effect	F	p	Partial η^2	Effect	F	p	Partial η^2
AS	6,983	,017	,291	AS	4,968	,040	,226
SST	23,744	,000	,583	SST	36,099	,000	,680
WML	22,892	,000	,574	WML	61,399	,000	,783
AS * SST	13,247	,002	,438	AS * SST	2,843	,110	,143
AS * WML	,962	,340	,054	AS * WML	9,037	,008	,347
SST * WML	6,511	,021	,277	SST * WML	0,148	,705	,009
AS * SST * WML	,000	1,000	,000	AS * SST * WML	3,412	,082	,167

3.4.2 FMRI RESULTS

3.4.2.1 ENCODING OF INFORMATION

WML. hiWML, as compared with loWML, led to increased activation in bilateral IFG (BA 44), SMA, insulae, precentral gyri, middle temporal gyri, and cerebella. Additionally, left IFG (BA 45), right middle frontal gyrus, left inferior parietal lobule, right supramarginal gyrus, and left middle occipital gyrus were activated stronger for hiWML during encoding (cf. Table 2). This is in line with previous WM studies (for a recent review, see Rottschy et al., 2012) documenting the data reliability of this study.

SST. The encoding of sentence fragments (SST+) elicited broadly increased activations as compared with the encoding of ungrammatical word strings (SST−), in a network including prefrontal areas (left BA 47, extending into BA 45 and dorsomedial PFC), bilateral middle temporal gyri, bilateral angular gyri and fusiform gyri, precuneus as well as bilateral hippocampi and adjacent parahippocampal gyri, right middle occipital gyrus, and right cerebellum (cf. Figure 3A, top, yellow; peak activations are depicted in Table 2). Ungrammatical word strings (SST−) led to stronger activations in the left intraparietal sulcus (IPS), right SMA (BA 6), and right superior frontal sulcus during encoding (cf. Figure 3A, top, blue; peak activations in Table 2). Because we were interested in the interplay between memory and sentence structure during the encoding period, interactions between SST and both WML and AS were calculated. The fMRI data did not reveal significant interaction effects between SST and WML. However, we found an interaction between SST and AS in bilateral SMA and intraparietal sulci, extending into superior as well as inferior parietal lobes (right supramarginal gyrus, cf. Table 2). Notably, participants did not yet start articulating during the encoding of words. The three-way interaction (SST × WML × AS) failed to show any significant results.

3.4.2.2 MAINTENANCE OF INFORMATION

WML. Higher WML led to increased activation in the right superior, middle, and inferior (BA 44) frontal gyrus as well as the left middle orbital gyrus, left inferior parietal lobule, and right superior parietal lobule extending into supramarginal gyrus during maintenance of items (cp. Table 3 and Figure 3-3B, activation increases of hiWML compared with loWML are depicted in cyan). These results are in line with previous literature on WM-related activations (for a recent meta-analysis, see Rottschy et al., 2012).

SST. In contrast to the encoding period, the presence of sentence structure (SST+) did not lead to additional activations during maintenance but to a relative reduction in brain activation in bilateral middle frontal (BA 46), left inferior frontal (BA 44/45), precentral (BA 6) as well as superior medial frontal and parietal regions (cp. Figure 3A, bottom, decreases in activation are depicted in blue color; all activation clusters and respective peaks are listed in Table 2).

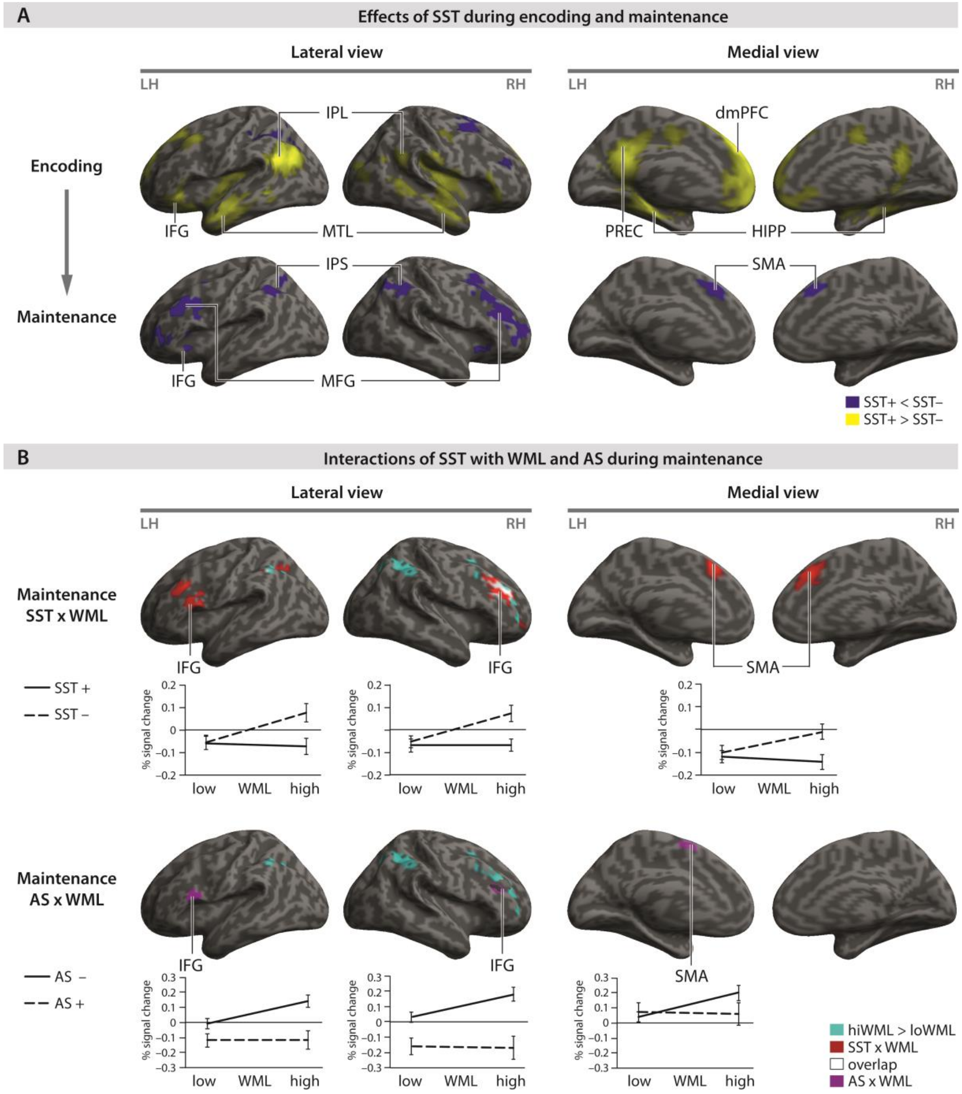


Figure 3-3: fMRI activation results. (A) Main effect of sentence structure during encoding (top row) shows significantly increased activations for structured, compared with unstructured memoranda in yellow-marked regions, and for unstructured, compared with structured memoranda in blue-marked regions. During the maintenance period, structured memoranda produce less activity (blue) than unstructured memoranda (bottom row). (B) Top: Significant activations for the main effect of WML (WML+ > WML–, cyan), the interaction of WML and sentence structure (red), and the overlap between effects (white). Diagrams below the activation maps display the results of ROI analyses (see Methods section) for the interaction clusters. Bottom: Significant activations for the main effect of WML (WML+ > WML–, cyan; identical to B) and the interaction of WML and AS (purple) as well as the results of ROI analyses for significant interaction clusters. All activations are rendered onto an inflated representation of the brain template provided by SPM8, with a threshold of p < .001 (corrected for cluster size, p < .001).

Error bars represent SEM (during maintenance phase). LH = left hemisphere; RH = right hemisphere; dmPFC = dorsomedial prefrontal cortex; HIPP = hippocampus; IFG = inferior frontal gyrus; IPL = inferior parietal lobule; IPS = intraparietal sulcus; MFG = middle frontal gyrus; MTL = medial temporal lobe; SMA = supplementary motor area.

Table 3-2: fMRI results. Activation clusters and peak voxels for all contrasts.

Brain region	**Hemisphere**	**BA**	**Cluster size (voxel)**	z_{max}	**MNI coordinates**		
					x	**y**	**z**
ENCODING: WORKING MEMORY LOAD HIGH > LOW							
Inferior frontal gyrus (p.Opercularis)	**L**	**44**	**4129**	**6,98**	**-51**	**14**	**16**
SMA	L	6		6,83	-3	14	52
SMA	R	6		6,83	9	17	46
Inferior frontal gyrus (p.Opercularis)	R	44		6,74	51	14	7
Insula	L			6,53	-30	23	1
Precentral gyrus	L	6		6,29	-39	-1	61
Insula	R			6,28	33	23	1
Precentral gyrus	L	6		6,26	-42	2	37
Putamen	L			6,14	-18	5	10
Superior frontal gyrus	R			5,64	27	8	52
Inferior frontal gyrus	L	47		5,59	-51	17	-5
Superior frontal gyrus	L			4,92	-24	8	67
Inferior frontal gyrus (p. Triangularis)	L	45		4,36	-51	35	1
Middle frontal gyrus	R			3,92	39	8	43
Inferior frontal gyrus (p.Opercularis)	R	44		3,85	39	8	25
Precentral gyrus	R	6		3,82	54	8	46
Middle temporal gyrus	L			3,59	-48	2	-20
Middle temporal gyrus	**L**	**21**	**506**	**6,45**	**-54**	**-46**	**10**
Cerebellum	**R**		**326**	**5,65**	**30**	**-61**	**-29**
Inferior parietal lobule	**L**		**390**	**5,22**	**-30**	**-58**	**43**
Middle occipital gyrus	L			5,06	-27	-70	37
Inferior parietal lobule	L			4,06	-48	-43	46
Middle frontal gyrus	**R**		**160**	**4,74**	**39**	**41**	**25**
	R		189	4,6	18	8	10
	R			4,09	12	-1	-2
Supramarginal gyrus (IPC)	**R**		**150**	**4,52**	**51**	**-31**	**46**
Cerebellum	L		61	4,48	-30	-64	-32
Middle temporal gyrus	R		54	4,22	48	-31	-2
ENCODING: CORRECT > INCORRECT SYNTAX							
Angular gyrus, IPC (PFm)	**L**	**40**	**6038**	**7.15**	**-48**	**-58**	**25**
Posterior Cingulate Cortex	L	23		6.58	-6	-52	25
Middle Temporal Gyrus	L	21		6.47	-54	-13	-17
Inferior Frontal Gyrus (p. Orbitalis)	L	47		6.31	-39	32	-14

Brain region	Hemi-sphere	BA	Cluster size (voxel)	z_{max}	MNI coordinates		
					x	y	z
Fusiform Gyrus	L	37		5.62	-27	-37	-17
Hippocampus (SUB)	L			5.25	-21	-25	-20
Inferior Temporal Gyrus	R	20		5.04	54	-16	-17
Angular Gyrus	R	39		4.98	57	-64	34
Hippocampus (CA)	R			4.84	27	-16	-17
Middle Temporal Gyrus	R	21		4.69	54	-1	-23
Supramarginal Gyrus	R	40		4.66	66	-46	31
Insula Lobe (Ig2)	R	-		4.59	36	-19	10
Hippocampus, Amygdala (LB)	L	-		4.53	-21	-7	-20
Rolandic Operculum	R			4.48	54	-22	22
Fusiform Gyrus	R	37		4.43	24	-40	-14
Superior Temporal Gyrus	L	38		4.36	-39	-16	-2
Superior Medial Gyrus	**L**	**9**	**2486**	**6.85**	**-9**	**50**	**34**
Mid Orbital Gyrus	L	10		6.04	-6	59	-11
Middle Frontal Gyrus	R	8		5.94	30	26	49
Superior Medial Gyrus	R	9		5.14	6	53	37
Rectal Gyrus	L	11		4.99	-3	44	-20
Anterior Cingulate Cortex	L	32		4.66	0	35	-8
Cerebellum	**R**	**-**	**66**	**4.99**	**27**	**-79**	**-32**
Middle Occipital Gyrus	**R**	**18/19**	**330**	**4.13**	**33**	**-82**	**13**
Fusiform Gyrus	R	37		3.88	24	-79	-11
Cuneus	R	18		3.22	15	-97	13
Middle Temporal Gyrus	R	22/19		3.11	48	-76	10
Precentral Gyrus	R	4		3.69	45	-13	49
ENCODING: SYNTAX INCORRECT > CORRECT							
Superior Frontal Gyrus	**R**	**4/6**	**139**	**4.74**	**21**	**8**	**52**
Inferior Parietal Lobule	**L**	**40**	**185**	**4.62**	**-39**	**-40**	**37**
Middle Occipital Gyrus	L	19		3.43	-27	-70	31
Middle Frontal Gyrus	**R**	**46**	**58**	**4.05**	**42**	**41**	**22**
ENCODING: SYNTAX X ARTICULATORY SUPPRESSION							
Inferior Parietal Lobule	**R**		**141**	**3.71**	**39**	**-49**	**43**
Supramarginal gyrus	R	40		3.66	42	-40	40
IPL	R	39		3.57	51	-34	52
Superior Parietal Lobule	**L**	**7**	**149**	**3.67**	**-27**	**-64**	**49**
Inferior Parietal Lobule	L	40		3.64	-45	-40	40
SMA	**L**	**6**	**107**	**3.46**	**-3**	**8**	**61**
Superior Medial Gyrus	R			3.41	6	23	43
SMA	R	6		3.19	6	11	52

Brain region	Hemisphere	BA	Cluster size (voxel)	z_{max}	MNI coordinates		
					x	y	z
MAINTENANCE: SYNTAX INCORRECT > CORRECT							
Superior Medial Gyrus	**L**	**6/8**	**214**	**4.86**	**-3**	**26**	**43**
Superior Frontal Gyrus	**R**	**6**	**702**	**4.79**	**21**	**14**	**49**
Middle Frontal Gyrus	R	46		4.74	42	38	28
Inferior Parietal Lobule	**L**	**40**	**241**	**4.74**	**-48**	**-55**	**49**
Superior Parietal Lobule	L	7		3.54	-33	-67	55
Inferior Parietal Lobule	**R**	**40**	**382**	**4.59**	**48**	**-52**	**52**
Superior Parietal Lobule	R	7		4.15	33	-70	52
Middle Frontal Gyrus	**L**	**4/6**	**64**	**4.43**	**-42**	**8**	**55**
Precentral Gyrus	L	4		3.15	-45	11	40
Insula Lobe	**R**		**55**	**4.20**	**39**	**23**	**-5**
Inferior Frontal Gyrus (p. Triangularis)	**L**	**45**	**274**	**3.82**	**-42**	**29**	**22**
Inferior Frontal Gyrus (p. Opercularis)	L	44		3.82	-48	11	28
Middle Orbital Gyrus	L	10/46	134	3.62	-39	44	-2

Most important for our present research question, we observed a reliable interaction between sentence structure and WML in left IFG (BA 44, extending into BA 45), right middle frontal gyrus (BA 46, extending into BA 45; largely colocalized with the main effect of WML), ACC (BA 32, extending into bilateral superior medial gyrus, BA 6), and left inferior parietal lobule (BA 40). A percent signal change analysis revealed that this effect was driven by the behaviorally most difficult condition, that is, hiWML in SST—ungrammatical word strings. This condition specifically elicited increased activations compared with all other conditions (cf. Table 3 and Figure 3B, top, red). Notably, maintenance-related activity in these areas did not differ between loWML and hiWML for SST+ items.

AS. AS led to significantly enhanced activations of motor cortex, auditory cortex, and cerebellum. Additionally, we found an interaction between AS and WML, in a rehearsal network containing activations in bilateral PFC, that is, right middle frontal cortex (BA 46), left inferior frontal cortex (BA 44/45), and SMA (cf. Figure 3B, bottom, purple). A percent signal change analysis revealed that hiWML induced larger activations in these areas during maintenance only in the session without AS. With AS, no load effects were found in the specified regions. The three-way interaction (SST, WML, and AS) did not yield any significant results.

3.5 DISCUSSION

This study explored the brain processes underlying the SSE. In line with previous work (Baddeley et al., 2009; Brener, 1940; Jefferies et al., 2004) the availability of sentence structure (SST) indeed improved working memory performance and response speed. Our results further showed that the SST-related performance improvement abolishes the behavioral effects of increased WML and AS, suggesting that the facilitatory effect of SST on memory formation reduces WML to a degree that allows participants to cope with substantially increased extents of input. These behavioral results are in line with the findings of Baddeley et al. (2009), who demonstrated that the SSE survives AS. Our fMRI data revealed that a complex pattern of enhanced and reduced brain activations across the encoding and maintenance phases goes along with the behavioral SSE. In the following sections, we will discuss these brain activation effects for the two phases consecutively.

3.5.1 SENTENCE STRUCTURE LEADS TO ENRICHED ENCODING

During encoding of sentence material into working memory (compared with ungrammatical word strings), sentence fragments led to less activity in the left inferior parietal sulcus. The left IPS has been discussed as a task-related attentional modulator in WM, which functionally connects to the right IPS in serial ordering tasks (Majerus et al., 2006) Following this line of interpretation, our data indicate that encoding a sentence fragment might require relatively fewer attentional resources than encoding and maintaining the exact sequence of an ungrammatical word string. Interestingly, in addition to this BOLD decrease, we found increased activity in a distributed system including prefrontal areas (left BA 47/45, dorsomedial PFC) as well as temporal and parietal regions and, bilaterally, the hippocampus and adjacent parahippocampal gyrus. Some of these regions have been associated earlier with semantic processing, whereas others have been linked to chunking during working memory encoding. The activation increases support the notion of enriched encoding processes that we hypothesized to support the SSE. Before discussing the nature of the engagement of these areas in detail, note that enhanced activation for the sentence material (the easier condition as indexed by behavioral performance data), although counterintuitive at first glance, is fully consistent with two earlier studies that investigated the processes involved in the chunking of working memory contents, that is, in combining individual items into larger bits of information to reduce WML (Bor et al., 2004b; Bor et al., 2003). Bor and colleagues (2004b; 2003) report, similar to our study, increased activation during encoding of structured material versus unstructured material. More specifically, across visually presented structured versus unstructured spatial sequences and auditorily presented structured versus unstructured number sequences, they showed encoding engagement of the right anterior PFC (BA 10), bilateral IFG (BAs 45 and 47, right BA 44), lateral temporal cortex (BAs 21 and 22, left BA 37), inferior parietal areas (BA 40) as well as left precuneus, right superior parietal gyrus, and the caudate nucleus. Some of these areas associated with chunking are also found in our study, such as inferior frontal areas, inferior parietal cortex, and precuneus. However, our data do not allow an unambiguous decision as to which areas in this study are activated for the SSE because of a domain-general contribution to chunking processes or because of language-specific processes. On the one hand, results from Bor et al. (2004b) point toward modality-independent chunking processes in the dorsolateral PFC. On the other hand, they also found specific (e.g., left inferior frontal, BA 47) activation for auditory– verbal material, suggesting that the engagement of frontal regions in our study may reflect language-specific processes during WM encoding.

Indeed, most of the brain regions showing SSE-related activation increase in our study are known from language studies, such as the left pars orbitalis (BA 47) for semantic processing (Chou et al., 2006; De Carli et al., 2007; Demb et al., 1995), dorsomedial PFC for semantic processing (Binder & Desai, 2011) and text comprehension (Yarkoni, Speer, & Zacks, 2008), middle temporal gyrus for semantic relatedness effects (e.g., bed, rest; McDermott, Petersen, Watson, & Ojemann, 2003), and sentence generation (Brown, Martinez, & Parsons, 2006), or the IPL, specifically the supramarginal gyrus for semantic processing and integration (Chou et al., 2006) and the angular gyrus for semantic memory retrieval (Binder et al., 2009). This is supported by our observation that the overall activation pattern strongly resembles the networks reported for semantic processing (Binder & Desai, 2011) as well as the one proposed for imagination and sequential pattern prediction (Buckner, 2010).

In this context, two questions arise: First, how might a stronger semantic network engagement (elicited by a comparison between sentence fragments and ungrammatical word strings, which only differed with respect to correct grammatical structure) contribute to working memory? Second, why are classical syntax-related areas like BA 44/45 (e.g., Friederici, Fiebach, Schlesewsky, Bornkessel, & von Cramon, 2006; Makuuchi et al., 2009; Santi & Grodzinsky, 2010) not involved?

With regard to the latter question, the aforementioned syntax studies compared sentences with more versus less complex syntactic structures, rather than simple sentence structures to ungrammatical word strings as in this study. Activations in BA 44/45 have been specifically attributed to the processing of complex syntactic structures—which was not required in this study. However, a simpler syntactic process, the formation of syntactic constituents, has also been related to activation in Broca's area (Pallier, Devauchelle, & Dehaene, 2011). In principle, it is conceivable that the use of function words in our ungrammatical word strings, which was necessary to keep the to-be-remembered items constant, led to the formation of short (two-word) constituents, attenuating a possible syntactic effect in Broca's area. The fact that constituents that can be built are much larger in the sentence condition speaks against this explanation. Syntactic features of simple sentences compared with word lists (e.g., noun lists) or ungrammatical word strings are thought to be processed in anterior temporal regions (e.g., Friederici, Meyer, & von Cramon, 2000; Humphries, Binder, Medler, & Liebenthal, 2006; Kaan & Swaab, 2002; Stowe et al., 1998; Vandenberghe, Nobre, & Price, 2002). This is in line with the activation observed in this study during the encoding of well-structured sentence fragments. Vandenberghe et al. (2002) compared syntactically correct items with their respective scrambled (thus ungrammatical) counterparts and found both effects of syntactic and semantic violations as well as their interaction in the left anterior temporal gyrus, leading the authors to suggest that this region is involved in deriving sentence-level meaning. However, others see anterior temporal regions to support combinatorial processes both in the semantic and syntactic domain (for a review, see Friederici, 2011).

Returning to the question of how additional semantic network activation in the present data might benefit memorizing, we find it particularly noteworthy that this prominent semantic activity pattern is observed in sentence fragments containing words that are relatively content-free when considered in isolation but that gain semantic value in the grammatical combination with other words (i.e., at the phrasal or sentence level). Take, for example, the high-load sample stimulus in Figure 1: "will er ihn heute Abend von" or, literally, "wants he him today evening from." This sentence fragment clearly establishes semantic relations, that is, the intention of one male agent to do something with or for another male patient at a specified point in time. Thus, although the details of a full semantic interpretation of the message are lacking, it is possible to build up a partial representation of meaning.

But how does the involvement of the semantic system contribute to a performance advantage in the present working memory task? One possible account is chunking of information. From cognitive psychology, we know that chunking requires the encoding of at least two hierarchical levels: item level and chunk level (Feigenson & Halberda, 2004). The grammatical information contained in the word list makes it possible to integrate the words (i.e., items) into a larger unit (i.e., chunk) that is specified by grammatical relationships and a basic meaning representation, as outlined above. This constitutes not only a syntactically but also a semantically enriched unit that contains agents and patients characterized, for example, by specific semantic roles. Additional encoding of sentence-level meaning of this kind, triggered by syntactic structure, might facilitate the following stages (i.e., maintenance and retrieval) of the working memory process. Whereas on the one hand, one might have expected greater effects of sentence structure in brain regions more directly related to syntactic processing, such as Broca's area, on the other hand, it is important to keep in mind that the linguistic chunking processes in our task design entail the integration of both syntactic and semantic sentential information. In addition to the semantic network, we find increased activation during encoding of sentence fragments in a brain structure that is not typically discussed in sentence comprehension—the hippocampus. Generally, the hippocampus is regarded as essential for long-term memory (LTM, Squire, 1992) and, more recently, also for working memory processes (Axmacher et al., 2010). Jefferies and colleagues (2004) proposed that immediate sentence recall might be better for sentences, because meaningful sentences receive additional support from LTM. Combining this insight with the observed activation of the semantic network, one possible explanation for our results may be that the information in a sentence might be enriched by semantic information stored in LTM. For example, sentence fragments such as "er hat sie gestern Abend von"/"he has her yesterday evening from" could be associated with LTM contents such as, for example, scripts of actions, emotions, or autobiographical memories such as "yesterday evening he took her to the train station," which might be an event recovered from memory that is not necessarily verbal. Indeed, the hippocampus has been linked to relational binding (i.e., storing items and their associations; for a review, see Moses & Ryan, 2006), specifically to multi-item maintenance in the visual domain (Axmacher et al., 2010), but also to semantic, associative processing (Henke, Weber, Kneifel, Wieser, & Buck, 1999). This assumed contribution of hippocampus to semantic-level binding is supported by the work of MacKay, Stewart, and Burke (1998). The authors report that patient H. M., who lost most of his hippocampi bilaterally undergoing an operation that was supposed to heal his epilepsy, was unable to recognize ambiguities in sentences, which the authors interpreted as reflecting a specific deficit regarding semantic-level binding.

All of the aspects mentioned above are plausible candidate mechanisms for building a memory chunk. Thus, a general explanation for the hippocampal activation found in our study might be relational binding of multiple items during the process of chunking. Because the sentence fragments used in this study primarily relied on function words that carry little content and that were frequently repeated within the experiment, the demand on explicit binding of the current item may have been particularly strong.

Apart from LTM enrichment or relational binding, there is empirical support for the idea that the hippocampus is involved in syntax processing. In an intracranial EEG recording study, Meyer et al. (2005) found a syntax effect in the hippocampus by comparing conditions where syntactic expectations were or were not met (i.e., syntactic violations), which the authors took as evidence that the hippocampus supports syntactic integration processes. The hippocampal response to syntactic violations seems to be in line with data showing that the hippocampus is also involved in processing prediction error signals (Kumaran & Maguire, 2006; Schiffer et al., 2012). Most specifically, it has been shown that most activity occurs in the hippocampus when predictions are violated within familiar sequences and not when the sequence is novel and unpredictable. Ungrammatical word strings can be regarded as unpredictable sequences, and it thus seems plausible that the hippocampus is only engaged when predictions are possible, that is, when processing stimuli with familiar syntactic structures.

However, because this study did not test these different explanations explicitly, we cannot evaluate them on the basis of our present results. Nonetheless, the results demonstrate that the hippocampus plays a role when language and working memory processes interact. A possible account for the SSE is thus that relational or predictive processing of linguistic memoranda—based on the rules of syntax and mediated by the hippocampus—facilitates short-term maintenance through combining the memoranda into a linguistically enriched chunk. Whether those processes fundamentally differ from sentence processing in the absence of a working memory task cannot be concluded from the present data. However, as the hippocampus is usually not reported for ordinary sentence comprehension, it can be speculated that some of the observed effects are specific to sentence encoding in a working memory task context.

3.5.2 SENTENCE STRUCTURE LEADS TO FACILITATED MAINTENANCE

We hypothesized that, because of enriched encoding of sentence fragments, as compared with ungrammatical word strings, less phonological rehearsal would be required for sentence fragments during maintenance. Indeed, our results reveal that, in contrast to encoding, maintenance of sentence fragments is accompanied by reduced brain activation compared with ungrammatical word strings in bilateral premotor (BA 6), SMA, right prefrontal (BA 46), and left inferior parietal cortex. Decreases in these areas have been considered to reflect facilitation of cognitive processes (e.g., the left inferior parietal lobule is linked to phonological storage, Awh et al., 1996; BA 46 to general maintenance of items during delay phases in WM tasks, Curtis & D'Esposito, 2003; and more generally, all of these regions are engaged in cognitive control, Kubler, Dixon, & Garavan, 2006). As already mentioned, although activity in the left IPS has been linked to the modulation of attention, it was proposed that the left and right intraparietal areas connect with each other when serial order is relevant during STM tasks

(Majerus et al., 2006). Thus, based on the bilateral IPS activity during the maintenance of ungrammatical word lists (SST−), we would argue not only that attention demands seem to be higher but also that order memory (as indicated by right IPS activity, cf. Marshuetz, Smith, Jonides, DeGutis, & Chenevert, 2000) is especially important when sentence structure is missing. In contrast, less effort might be necessary to keep the order of words in mind when sentence structure is available.

In line with these findings, facilitation of cognitive demands indeed might be one of the main differences between processing sentence fragments versus ungrammatical word strings in this study, because (a) the sentence fragments used in the stimulus set are highly frequent in everyday language and (b) maintenance of sentence fragments is, as concluded above, supported by a semantic representation generated during encoding. As we used ungrammatical strings including mainly function words rather than classical word lists (e.g., lists consisting of nouns or adjectives exclusively), the possibility for building semantic associations is extremely limited in the SST− condition in our case. Moreover, the ungrammatical word strings we used are not only infrequent in everyday language, but they violate phrase structure rules. Both of these properties may have further contributed to the facilitation for sentence fragments. It seems unlikely that the direction of the facilitatory effect would have changed if classical word lists had been used, but further investigations could specify how the facilitatory effect would be modified by using ungrammatical word order versus unrelated word lists.

Additional to the decreased brain activation induced by sentence structure and to prototypical rehearsal-related activations (BA 46, SMA, BA 40; e.g., Zarahn, Rakitin, Abela, Flynn, & Stern, 2005) for high load versus low load (cf. Paulesu, Frith, & Frackowiak, 1993), we found a significant interaction of sentence structure and WML in the left Broca's area, bilateral BA 46, and SMA during maintenance. This interaction was driven by the ungrammatical word strings: A load effect in these areas was observed exclusively for ungrammatical strings, not for sentence fragments, which, interestingly, resembles the pattern of results for behavioral accuracy (Figure 2A). Thus, our findings suggest that, if sentence structure is available, sufficient resources are available to cope with increased demands on the working memory system—for example, when the load on working memory is increased. Thus, we conclude that the presence of syntactic structure in verbal memoranda reduces the demands on neural systems involved in working memory maintenance— presumably because of the chunking processes discussed in the previous section.

In addition, we aimed to discover whether the SSE is affected by the availability of the phonological rehearsal mechanism. Although we found an interaction between SST and AS in the behavioral data, that is, increased error rates in conditions with AS only for ungrammatical word strings but not for sentence fragments, we did not find a neuronal counterpart of this interaction effect during the maintenance phase in our fMRI data. Independent of the syntactic manipulation, the main effect of AS during maintenance revealed significant activations of motor cortex, auditory cortex, and cerebellum. These results are expected given the literature regarding the role of auditory and motor/premotor cortex in articulation (cf. Wildgruber, Ackermann, Klose, Kardatzki, & Grodd, 1996; Yetkin et al., 1995) and motor timing for the cued production of syllable strings supported by the cerebellum, which are said to be involved while "computing the temporal parameters of incoming sensory stimuli" (Penhune, Zatorre, & Evans, 1998). Thus, although the prevention of rehearsal via concurrent articulation was successful, the fMRI data provide no evidence that the facilitation caused by sentence structure is necessarily affected by the availability of rehearsal mechanisms during the maintenance of information.

Combining the results from both encoding and maintenance, an integration of our results into current working memory models is still lacking. In the following paragraph, we will discuss our results in the light of two major models explicitly referring to sentence structure phenomena in memory tasks.

3.5.3 SENTENCE STRUCTURE UNBURDENS WORKING MEMORY

Neither general psychological models of working memory (such as Baddeley's multicomponent model (Baddeley, 2012) or process-based models (e.g., Cowan, 1999; Zhou et al., 2007) nor more specific models of sentence recall (Jefferies et al., 2004; Potter & Lombardi, 1990, 1998) directly address the neuronal mechanisms underlying encoding and maintenance of sentences. Nevertheless, our results provide support for some of the assumptions of the latter class of models. First, the CRH states that a "sentence is regenerated in immediate recall from a representation of its meaning, using recently activated words" (Potter & Lombardi, 1990, p. 633) and later was expanded to syntactic priming, which means that the encoding of the syntactic surface structure facilitates their reproduction in immediate recall (Potter & Lombardi, 1998). The authors argue that, instead of maintaining a "surface" representation such as a phonological string, in sentences, the preactivation of words and the generation of a semantic interpretation during encoding may be sufficient for facilitating later recall. Indeed, we found semantic network activation for sentences already during the encoding of information, which provides support for the proposed importance of semantic processes during encoding. Furthermore, the neuronal deactivation pattern for sentence fragments as compared with ungrammatical word strings during maintenance is at least consistent with the CRH, which assumes no specific maintenance mechanisms for sentences. However, our results go beyond this assumption and suggest that more elaborate encoding processes in fact unburden neural systems supporting maintenance. Finally, because the current study focused on the encoding and maintenance of information, we cannot provide direct evidence for the third part of the CRH, namely, the recall of meaning and rebuilding of sentences using previously activated words.

Whereas Potter and Lombardi focus mostly on the regeneration of sentences during recall, Baddeley and colleagues (2009) attribute the advantage of sentential material to the automatic chunking of sentences during encoding. The authors state that sequential redundancy, that is, the familiarity with specific word combinations, makes it easier to combine them in the very same order again—which would thus also benefit working memory. But even if one acknowledges that "sequential redundancy" contributed to better working memory encoding of sentences in our experiment, still, the question remains unresolved how this facilitation effect is mirrored in the brain. In general, easier tasks evoke less brain activity. Following this line of argumentation, one would have expected less activation for sentences than for word lists. Instead, we found an interesting pattern of stronger activations during encoding and activation decreases during the maintenance of sentence fragments (compared with ungrammatical word strings) in our data. Thus, from our data, we conclude that the effect of sentence structure on working memory (possibly relying on sequential redundancy) is reflected in this temporal interplay of brain activity during encoding and maintenance. In short, the memory facilitation for SST+ is not accompanied by less overall brain activity but rather by enhanced activity during LTM-enriched encoding followed by activation decreases during the less effortful maintenance phase. Process models of working memory therefore do not explain the present findings well as no sustained sentence-specific activation was found during the maintenance phase.

3.5.4 CONCLUSION

This study investigates for the first time the neural mechanisms underlying the SSE. Sentence structure activates a network of prefrontal, middle temporal, hippocampal, and inferior parietal brain areas during encoding. Therefore, we propose that the brain mechanisms underlying the SSE most probably involve (a) chunking, because of easier, hippocampally supported, relational binding of items according to grammatical rules, and (b) the association of items with LTM contents during encoding. According to our data, this elaborated encoding process results in a semantically enriched memory representation, subsequently facilitating the maintenance of information in working memory: Sentence structure leads to less engagement of rehearsal-related areas, specifically the left IFG, SMA, and right middle frontal gyrus, in the maintenance phase of the working memory task. Complementing earlier behavioral evidence, this study delineates the interplay between enriched encoding and resulting reduced maintenance demands that underlies the SSE.

3.5.5 ACKNOWLEDGMENTS

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4 COMBINED EYE TRACKING AND FMRI REVEALS NEURAL BASIS OF LINGUISTIC PREDICTIONS DURING SENTENCE COMPREHENSION[8] (MANUSCRIPT 2)

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4.1 ABSTRACT

It is widely agreed upon that linguistic predictions are an integral part of language comprehension. Yet, experimental proof of their existence remains challenging. Here, we introduce a new predictive eye gaze reading task combining eye-tracking and human functional magnetic resonance imaging (fMRI): Participants read different types of word sequences (i.e., normal sentences, meaningless jabberwocky sentences), up to the pre-final word. The target word was displayed with a temporal delay and its screen position was dependent on the syntactic word category (nouns vs. verbs, e.g., in the upper vs. lower right corner). During the delay, anticipatory eye-movements into the correct target word regions indicated the existence of linguistic predictions. FMRI analysis was time-locked to anticipatory eye-movements, in order to extract the neural substrate of the linguistic prediction, in contrast to a non-word list control condition that allowed no predictions. Prediction of linguistic structure was supported by a distributed network of cortical and subcortical brain regions including language systems, basal ganglia, thalamus, and hippocampus. Specific analyses indicate that prediction of word category relies on classical left-hemispheric language systems involving Brodmann's area 44/45 in the left inferior frontal gyrus, posterior and anterior left superior temporal areas, but also the dorsal caudate nucleus. Predictions of specific words, in contrast, recruited more widely distributed temporal and parietal cortical systems, and more so in the right hemisphere. Our results support the importance of linguistic predictions for sentence processing and demonstrate the validity of the predictive eye gaze paradigm for measuring linguistic predictions and their neural substrates.

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[8] This chapter corresponds to the submitted manuscript (preprint) of Bonhage, C. E., Mueller, J. L., Friederici, A. D., & Fiebach, C. J. (2015, in press). Combined eye tracking and fMRI reveals neural basis of linguistic predictions during sentence comprehension, *Cortex*, http://dx.doi.org/10.1016/j.cortex.2015.04.011.

4.2 INTRODUCTION

Language-based communication involves the exchange of enormous amounts of highly structured sensory information in very short time windows. One way to efficiently handle the ensuing cognitive demands is to process language in a proactive way by relying on predictions. Predictive processing is believed to be a fundamental principle of brain function (Bar, 2007; Friston & Kiebel, 2009; Huang & Rao, 2011; see Rao & Ballard, 1999). It is assumed that based on previous experiences, the brain generates hypotheses about the external world and thus predicts upcoming sensory events. Only when the actual input diverges from these predictions, sensory inputs are communicated in a bottom-up fashion to hierarchically higher systems, so that predictions can be adjusted. By minimizing such prediction error signals, the predictive brain reduces the demands on bottom-up processing of redundant information, thereby maximizing the efficiency of perception.

Language processing has only recently been linked explicitly to predictive coding (Arnal & Giraud, 2012; Jakuszeit et al., 2013; Sohoglu et al., 2012). In the case of language, such predictions would be based on grammatical rules of language (syntax) but also on information provided by contextual meaning (semantics). A recent (psycho-) linguistic theory proposes that the “surprise” about a specific word decreases when more constraining context information becomes available, for example over the course of a sentence (Levy, 2008; Smith & Levy, 2013). Surprise, however, is conceptually equivalent to prediction error (cf. Schwartenbeck et al., 2013), which provides an interesting link between fundamental neuroscientific theorizing and current psycholinguistic models (see also Dikker et al., 2010; Pickering & Garrod, 2013 for further discussions of the importance of predictive mechanisms during language processing; Van Petten & Luka, 2012). However, it has been challenging to measure linguistic predictions, because the predictive process as such is not directly accessible to observation. Neurocognitive language research relies widely on violation paradigms that cannot ultimately separate predictions from ongoing sensory processing (e.g., Kutas & Federmeier, 2011), thus evidence for linguistic predictions remains indirect.

To more directly measure linguistic predictions, we developed a novel “predictive eye gaze reading task” for sentence processing: Syntactic categories (i.e., nouns vs. verbs) of sentence-final words were associated with specific positions on the computer screen while measuring anticipatory eye movements to assess the existence and timing of predictions. Timing information derived from anticipatory eye movements, in turn, informed the analysis of simultaneously acquired fMRI data. We hypothesized that predictions about upcoming syntactic structure (here, word category) are reflected in anticipatory eye movements into the spatial location of the expected target word category. As the predictive coding framework holds that these predictions are generated by language-related cortical systems, we expected that the linguistic prediction of word category should rely on syntax-related brain systems (such as Broca's area; Fiebach & Schubotz, 2006; Friederici, 2002), while the prediction of specific words should additionally recruit brain regions involved in semantic processing (cf. Binder et al., 2009). In addition, we assumed that more domain-general systems involved in various types of sequential processing contribute to linguistic predictions as well.

4.3 METHODS

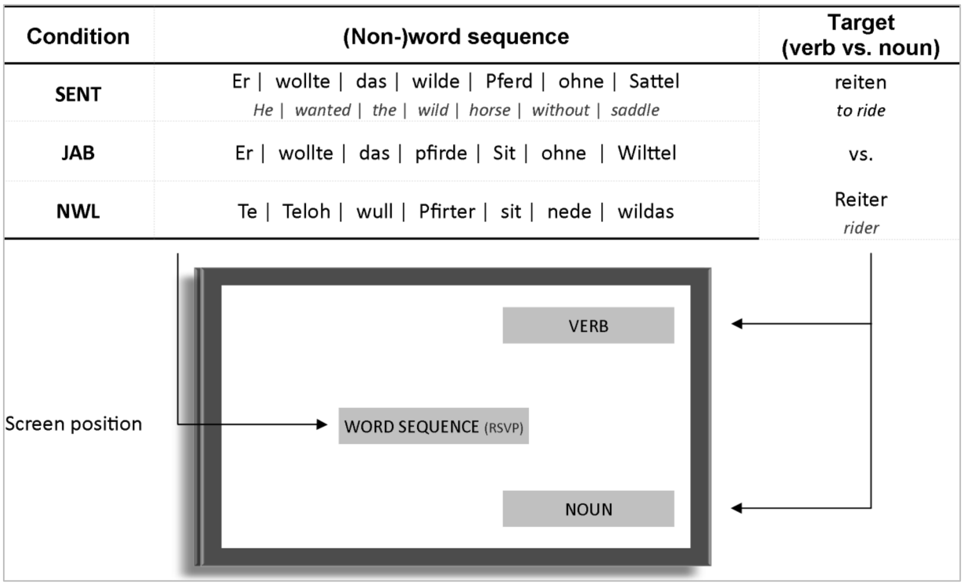
4.3.1 PARTICIPANTS

Twenty-three native German speakers without a known history of dyslexia or other psychiatric or neurologic diseases participated after giving written informed consent in accordance with the Declaration of Helsinki. All participants were right-handed according to their scores on the Edinburgh handedness inventory, and were financially compensated with 7 Euro per hour. Due to technical problems (i.e., eye tracking data loss) and/or excessive movement during fMRI measurements, 5 participants had to be excluded from the reported analyses. The remaining 18 participants (nine female) were aged between 22 and 33 (mean age = 26.6; SD = 2.8).

4.3.2 EXPERIMENTAL DESIGN AND STIMULI

The effect of predictions on language processing was examined in a within-subject design, in which the processing of normal sentences (SENT), which allowed predictions of upcoming words based on both syntactic structure and semantic content, was compared (a) to the effect of word category predictions in so-called jabberwocky sentences (JAB), i.e. sentences in which grammatical structure was retained while content words were replaced with pronounceable non-words following German morphophonemic rules, and (b) to the processing of pronounceable non-word lists (NWL) which allowed no predictions during their processing. The final word was a real word in all conditions (cf. Figure 4-1 for example items for all three conditions). Each condition consisted of 60 stimuli, summing up to a total of 180 trials.

The number of syllables of word sequence and target words was matched between all three conditions. A pilot study with 20 German natives (10 female; mean age = 24.4 years; SD = 2.4) was conducted investigating the cloze probability for SENT items as well as the probability of the target word to belong to a certain word category (i.e., verb or noun) for all conditions (i.e., SENT, JAB, and NWL). Results revealed that all normal sentences (SENT) had a cloze probability of 89.83 % on average (SD = 13.4; minimum CP: 65%) at the last word. Additionally, in both SENT and JAB items the word category of the sentence final (i.e., target) word was correctly predicted with high probability (SENT: mean = 99.16, SD = 1.9; JAB: mean = 96.58, SD = 5.6), while NWL items did not elicit correct predictions (mean = 32.33, SD =12.1). Given that JAB and NWL were created from the SENT items, there was a potential danger of orthographic priming effects (specifically, the recognition of the normal sentence in one of the other conditions due to orthographic similarity) potentially leading to - at least implicit - semantic expectations about the target word in the JAB and NWL conditions as well. To avoid such effects, participants were presented with different stimulus lists in SENT vs. JAB and NWL: We divided the originally pre-tested stimulus set (360 items; see above) into two subsets A and B (180 items each) that were exactly matched for syllable count and did not significantly differ in terms of word sequence length of all items (in letters; (t(179) = -0.01, p = .98) or cloze probability of sentence items (t(29) = 0.19, p > .99). In the present study, one half of the participants were presented with sentences from subset A and jabberwocky items and non-word lists from subset B, while the other half was presented with the respective opposite subsets (i.e., sentences B, jabberwocky A, and non-word lists A). Each item was presented twice, once with a grammatically correct target word, once with a wrong target word. Participants were asked to judge the grammatical validity of the presented target word given the previous word



Condition	(Non-)word sequence	Target (verb vs. noun)
SENT	Er | wollte | das | wilde | Pferd | ohne | Sattel *He | wanted | the | wild | horse | without | saddle*	reiten *to ride*
JAB	Er | wollte | das | pfirde | Sit | ohne | Wilttel	vs.
NWL	Te | Teloh | wull | Pfirter | sit | nede | wildas	Reiter *rider*

Figure 4-1: Design, example item, and screen positions. RSVP, rapid serial visual presentation; cf. Figure 4-2 for timing information.

sequence; in terms of semantics the target word always fitted the previous word sequence (cf. Figure 4-1). For non-word lists items, where participants could not be sure about the valid target word category, we instructed them to decide quickly according to their gut feeling.

4.3.3 EXPERIMENTAL PROCEDURES

All participants completed questionnaires regarding their caffeine/nicotine/alcohol consumption and sleep patterns before entering the pre-experimental training session (~15 min) and finally the combined fMRI and eye tracking experiment (~ 1 hour). As illustrated in Figure 4-2, during both training session and fMRI experiment each trial consisted of three consecutive phases. During the trial, possible word positions (i.e., centered, upper/lower right corner) were indicated by three grey boxes. During the word sequence presentation, the seven cue words (or non-words) were presented one by one for 500ms each in the center of the screen (word sequence presentation; WSP). In the sentence and jabberwocky conditions, these seven words built up the sentence context based on which the participants should expect the word category of the target word. The WSP was followed by a prediction gap (PRED; 4.5 – 5.5s jittered, 5s on average), where only the three grey boxes were presented visually, indicating possible word positions on the screen. Finally, in the task phase, the target word was presented for 3.5 seconds in either the upper or lower right corner, depending on the respective word category (e.g., verbs in upper/nouns in lower right corner) and participants had to decide, whether the target was a grammatically correct continuation of the word sequence presented before (TASK).

Note that the association between target word category (verb vs. noun) and position on the screen (upper vs. lower right corner) was firmly established during the training procedure; at the beginning of the fMRI experiments all participants were aware that verbs and nouns would consistently appear in the respective corner throughout the entire experiment. Positions of verb and noun targets were counterbalanced across participants.

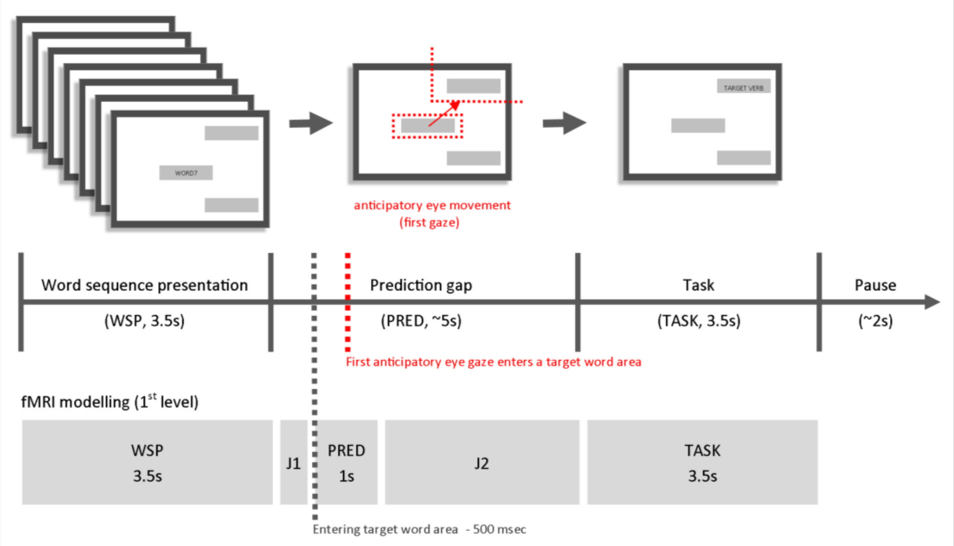


Figure 4-2: Trial description and modelling of fMRI regressors.

4.3.4 DATA ACQUISITION

Behavioral data (i.e., button presses and eye movements) were assessed using two magnet resonance compatible response boxes, an ASL eye tracker (ASL Eye-Trac 6, www.asleyetracking.com/site/Products/EYETRAC6Series/LongRangeOptic/tabid/69/Default.aspx), and the stimulus presentation software Presentation® (Version 14.1, www.neurobs.com). FMRI data were acquired on a Siemens TIM Trio 3 Tesla MR Scanner. Prior to the acquisition of functional data, a T1-weighted 3D MP-RAGE sequence (as described in Mugler & Brookeman, 1990) was measured for coregistration (inversion time = 650 ms; repetition time of complete sequence cycle = 1300 ms; echo time, TE = 3.93 ms; repetition time of the gradient-echo kernel (snapshot FLASH; cf. Haase, 1990); field of view, FOV = 256 mm x 240 mm; sagittal orientation; 2 acquisitions; spatial resolution = 1 x 1 x 1.5 mm). During the experiment, functional MRI data was collected by continuous scanning of 430 scans for each of the three experimental runs. The experiment was split into 3 runs (with a duration of approximately 15 minutes each) in order to retain an option to recalibrate the eye tracker between runs if necessary. For fMRI, we used a gradient-echo echo-planar imaging (EPI) sequence with a TR of 2000 ms (TE = 30 ms, flip angle = 90°, acquisition bandwidth = 116 kHz), acquiring a matrix of 64x64 (FOV = 192mm) which results in an in-plane resolution of 3 mm^2. Whole brain coverage was achieved by assessing 30 slices with a slice thickness of 3 mm plus an inter-slice gap of 1 mm.

Behavioral data. Response times and accuracy were analyzed using SPSS (Version 19, www.ibm.com/software/de/analytics/spss/). The dependency of response times and accuracy of responses on the within-subjects factor STRUCTURE (levels: SENT, JAB, and NWL) was estimated performing general linear model (repeated measures) analyses as well as paired t-tests for the respective planned post-hoc comparisons (Bonferroni corrected).

Eye tracking data. Two eye tracking parameters were estimated for the current paradigm. The first parameter, namely the time until the first saccade reached a target word area (TWA, possible screen positions of the target words, i.e. upper/lower right corner), was operationalized as the time it took the participants to move their eye gaze from the center of the screen (where the last word of the word sequence is presented) to one of the TWAs.

$$\begin{aligned} &time\ until\ the\ first\ saccade\ reached\ the\ target\ word\ area\ (in\ msec) \\ &\qquad = time\ point\ when\ the\ eye\ gaze\ enters\ the\ TWA \\ &\qquad - start\ of\ 7th\ word\ of\ the\ preceding\ word\ sequence \end{aligned}$$

The second eye tracking parameter of interest was the fixation time of the grammatically correct and thus predictable TWA (cp. Figure 4-2), compared to the time spend in either of the two TWAs:

$$\begin{aligned} &fixation\ time\ (in\ \%) \\ &\qquad = \frac{fixation\ time\ of\ predictable\ TWA}{fixation\ time\ of\ predictable\ TWA + fixation\ time\ of\ other\ TWA} * 100 \end{aligned}$$

The percentage of fixation time is also taken as an indicator for the confidence of the prediction, since participants who are certain about the target word category are hypothesized to spend more time gazing anticipatorily at the grammatically valid TWA as compared to the invalid TWA.

After imputing missing eye tracking data (<25%) using the multiple imputation algorithm implemented in SPSS 19, we estimated general linear models (repeated measures) with the within-subjects factor STRUCTURE (levels: SENT, JAB, and NWL) for both the time until the first saccade reached the target word area and fixation time of the grammatically valid target word area.

MRI data. Functional data were preprocessed and analyzed using the MATLAB-based SPM software package (statistical parametric mapping, version 8.4, provided by the Wellcome Trust Centre for Neuroimaging, London). Preprocessing steps in their respective order included (1) correcting for head motion via realignment and coregistering the EPI images to the subjects' T1-weighted structural image, (2) slice timing correction with consecutive reslicing, and (3) spatially normalizing into the standard stereotactic space provided by the Montreal Neurological Institute (MNI; implemented in SPM8). The data were then spatially smoothed with a 4 mm full-width at half maximum isotropic Gaussian kernel to increase the signal-to-noise-ratio.

In order to include the timing information about the predictive process gained from eye tracking into the individual fMRI model, we chose the time until the first saccade reached the target word area as an estimate. As mentioned above, this parameter is taken as an indicator for the confidence and ease of the anticipation, hypothesizing that if the participants are very confident about the target word category they expect, they will shift their eye gaze to the respective corner very fast (and vice versa). It contains information about the timing of the prediction, since participants presumably are moving their eyes into the target region when they (a) decided that the target word must belong to a specific word category and shift their gaze into the respective TWA (i.e., in normal and jabberwocky sentences) or (b) randomly move their eyes into the one or the other TWA in non-word lists. However, in all conditions an eye movement is produced; therefore, the motor and primary visual activity due to simple saccades should be present in all conditions and cancel out when contrasting them. We further reasoned that the prediction is already in progress when the target word region (which is an enlarged TWA, cf. upper panel of Figure 4-2) is entered. However, since the path of the saccade into the TWA was not always straight, the prediction might not have built up right when the eye gazes leave the center region, but rather unfold over the course of the saccade. Thus we chose to use the time point when the eyes enter the target word region minus 500 milliseconds as the starting point for the supposed prediction process; going back in time any further would have introduced a confound, because there would have been a significant overlap of prediction phase and presentation of the seventh word for sentences, but not for jabberwocky or non-word lists (see Results).

Therefore, at the individual subject level, we modeled word sequence presentation (WSP; 3.5s), jitter1 (J1; onset = offset of WSP, duration until start of prediction phase), prediction (PRED; Onset = the time until the first saccade reached the target word area - 500ms, duration = 1 second), jitter2 (J2; onset = offset of PRED, duration until the task phase starts), and task (TASK; 3.5s) against an implicit baseline (cf. Figure 4-2, lower panel). Note that critical trial phases WSP, PRED and TASK (modeled per condition) were separated by the jitter phases (J1, J2, modeled across conditions) in order to reduce the multicollinearity between the critical trial phases: By introducing jitter between phases, the hemodynamic responses of the adjacent phases overlapped differentially (cf. Schon, Quiroz, Hasselmo, & Stern, 2009). Additional regressors in the general linear model took into account error trials (independent of condition, modelled as entire trial), instruction screens (indicating start, pauses and end of the experiment) as well as head movement (i.e., six realignment parameters). Implicit baseline contrasts for all conditions during the prediction phase (PRED) were used for 2nd level analysis (random effects analysis, t-tests).

Our analysis focused on two aims: To extract the neural activation underlying the anticipation of a word category, and to reveal the differences between predicting a word category and predicting a meaningful word. To investigate the latter question, we contrasted normal to jabberwocky sentences. However, to extract the brain areas supporting word category prediction, two analysis steps were performed. First we contrasted both conditions providing syntactic structure (i.e., SENT and JAB) to NWL separately (t-tests: SENT > NWL and JAB > NWL). Afterwards, we performed a conjunction analysis of the two t-tests in order to find the common neural substrate of both conditions allowing for word category prediction (SENT, JAB) compared to the condition without syntactic cues (NWL). A cluster threshold of 12 voxels was applied to all contrasts in order to correct for multiple comparison; the minimal cluster size was estimated with a Monte Carlo simulation with 1000 iterations using the software package AlphaSim (Ward, 2000; parameters: -nxyz 64 64 30, -dxyz 3 3 3, -fwhm 4, -iter 1000, -pthr 0.001).

4.5 RESULTS

4.5.1 BEHAVIOR

Response times. As depicted in Figure 4-3, a general linear model (GLM, repeated-measures) showed that response times differed between conditions ($F(2,16) = 18.46$, $p < .001$, $\eta^2 = .70$). Specifically, planned post-hoc paired t-tests revealed that participants responded faster to sentences (SENT) as compared to jabberwocky (JAB; $t(17) = -6.10$, $p < .001$), and to non-word lists (NWL; $t(17) = -4.91$, $p < .001$). In addition, JAB was answered faster than NWL ($t(17) = -3.78$, $p = 0.001$).

Accuracy. Accuracy was well above chance level in SENT and JAB and did not differ from chance level in NWL ($t(17) = 2.15$, $p = 0.46$; Figure 4-3). A repeated-measures GLM revealed

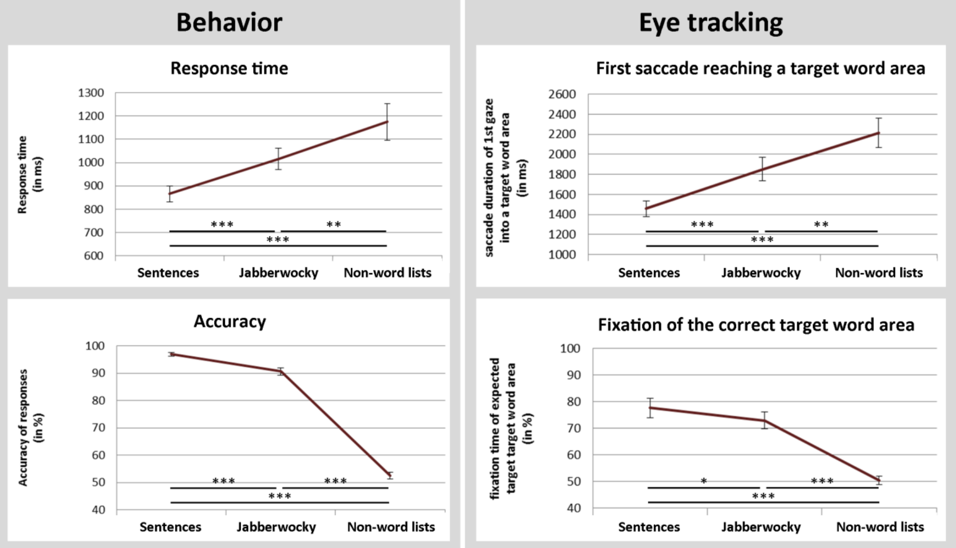


*Figure 4-3: Behavioral performance and anticipatory eye movements. The time until the first saccade reached the target word area (TWAs): Measuring the time from the onset of seventh word of the word sequence (in the center of the screen) until the participants' gaze enters one of the target word areas (upper/lower right corner of the screen). Fixation of the grammatically correct target word area: Fixation of grammatically valid target word area / (Fixation of grammatically valid target word area + Fixation of grammatically invalid target word area)*100. *, p < .05; **, p < .01; ***, p < .001. Error bars represent standard error of mean.*

that conditions differed in terms of accuracy (F(2,16) = 963.92, p < .001, η^2 = .99). Planned post-hoc comparisons showed that participants' performance for SENT was significantly higher than for JAB (t(17) = 4.90, p < .001) and NWL (t(17) = 44.09, p < .001). Additionally, accuracy dropped significantly from JAB to NWL (t(17) = 22.16, p < .001). To sum up, results indicate that behavioral performance was highest for sentences, reduced for jabberwocky sentences, and - as necessarily expected - at chance level for non-word lists.

4.5.2 EYE TRACKING

As detailed in the Methods section, we investigated two eye tracking parameters indicating prediction processes during the delay between context and target word presentation. First, the time until the first saccade reached the target word area was measured by calculating the time spent from the onset of the seventh word of the word sequence in the center of the screen until the gaze of the participant entered one of the target word areas (TWA, i.e., the areas marked in dashed lines in the upper and lower right corner of the screen, cf. Figure 4-2). This latency should be minimal in a condition eliciting a high expectation with respect to the word category of the target word. As depicted in Figure 4-3, results of a repeated measures GLM revealed significant differences between conditions (F(2,16) = 20.08, $p < .001$, $\eta^2 = .72$); planned post-hoc comparisons demonstrated that the first anticipatory saccade reached one of the target word areas earlier after being presented with normal sentences than jabberwocky sentences (t(17) = -5.63, $p < .001$) and non-word lists (t(17) = -6.11, $p < .001$). Furthermore, the target word area was fixated more rapidly in jabberwocky items compared to non-word lists (t(17) = -3.47, $p < .01$). Thus, participants' eye gaze reached the target word areas especially fast for sentences, followed by jabberwocky items, and slowest for non-word lists.

Although the latter result already hints at a predictive process, it remained possible that participants changed their opinion over the course of the prediction phase or corrected their initial saccade after entering one of the target word areas. Therefore, we assessed a second parameter indicating how long they fixated the grammatically valid target word area (i.e. the fixation time, the relative time spent in the target area where the grammatically correct target was expected to appear in relation to the overall time spent in any of the target regions). Again, a repeated measures GLM revealed a significant difference between all conditions (F(2,16) = 36.68, $p < .001$, η2 = .82). Post-hoc comparisons revealed a higher percentage of correct target word area fixation times in normal sentences than in jabberwocky sentences (t(17) = 2.23, $p < .05$) or non-word lists (t(17) = 8.34, $p < .001$). Figure 4-3 illustrates that the fixation time in the correct target word area was also longer for jabberwocky compared to non-word list items (t(17) = 8.27, $p < .001$). While the fixation times indicated a clear preference of the grammatically valid target word area in normal and jabberwocky sentences, it was – expectedly – at chance level for non-word lists (t(17) = 0.21, p = 0.837). Summing up, results indicate that for both parameters, i.e., the time until the first saccade reached the target word area and the correct target fixation time, anticipatory eye movement performance was most decisive for sentences, slightly less so for jabberwocky sentences, and lowest (i.e., at chance level) in non-word lists.

4.5.3 FUNCTIONAL MRI RESULTS

We used fMRI to identify the brain systems involved in linguistic predictions. To this end, we pursued two major objectives: (1) to isolate the brain systems engaged in generating syntactic (i.e., word category-based) predictions and those systems supporting the lexically specific prediction of meaningful words based on the semantics of the preceding sentence context, and (2) to identify domain-independent neural systems that are generally involved in generating linguistic predictions during sentence comprehension based on sentence structure.

To answer the first question, we compared purely syntactic predictions in which the word category, but not the specific word, can be predicted (i.e., in meaningless jabberwocky sentences) to the prediction of a specific meaningful word in the context of (semantically) normal sentences (see Table 4-1). If linguistic predictions had to rely exclusively on word *category* information (i.e., in jabberwocky sentences), participants responded with increased activity bilaterally in inferior and middle frontal gyri extending into orbital sulci (bordering anterior and posterior orbital gyri), with a clear pronunciation of left hemispheric involvement, insulae and superior temporal sulci as well as in left SMA, left precentral gyrus, left angular gyrus, right caudate nucleus, and right anterior cingulate (Figure 4-4A, red). In contrast, several cortical and subcortical areas showed stronger activity for full semantic as compared to purely syntactic (i.e., word category) predictions. These included, at the cortical level, bilateral superior frontal gyri, right precentral and left postcentral gyrus, right rolandic operculum and medial temporal pole, bilateral insulae, left superior temporal, right middle temporal and bilateral inferior temporal gyri; bilateral fusiform and supramarginal gyri as well as right lingual gyrus, superior, and inferior occipital gyri, as well as bilateral middle occipital gyri . In addition, subcortical structures (i.e., bilateral hippocampi, thalami, putamen, cerebella, middle cingulate, and right anterior cingulate) displayed increased activation for semantic word prediction (Figure 4-4A, yellow).

The second research question regarding the common neural substrates of word and word category predictions was tackled by a two step-procedure: First, we contrasted each of the two conditions providing syntactic structure (i.e., normal and jabberwocky sentences) with the condition in which linguistic prediction is not possible (i.e., non-word lists; cf. Figure 4-4B). Subsequently, a conjunction analysis (cf. Figure 4-4C) was performed to extract common brain activation for predictive processes. Results of this conjunction analysis reveal the engagement of a widely distributed cortical network of brain areas supporting word category predictions in the context of both normal and meaningless jabberwocky sentences, including bilateral precentral sulci as well as, in the left hemisphere, the opercular portion the precentral sulcus, the so-called rolandic operculum. Additionally, in the left hemisphere the conjunction analysis revealed activation increases in insula, posterior superior temporal sulcus, supramarginal gyrus, and in subcortical areas including the hippocampi, putamen, thalami, and cerebella as well as the left head of the caudate nucleus (cf. Table 4-2 for more details).

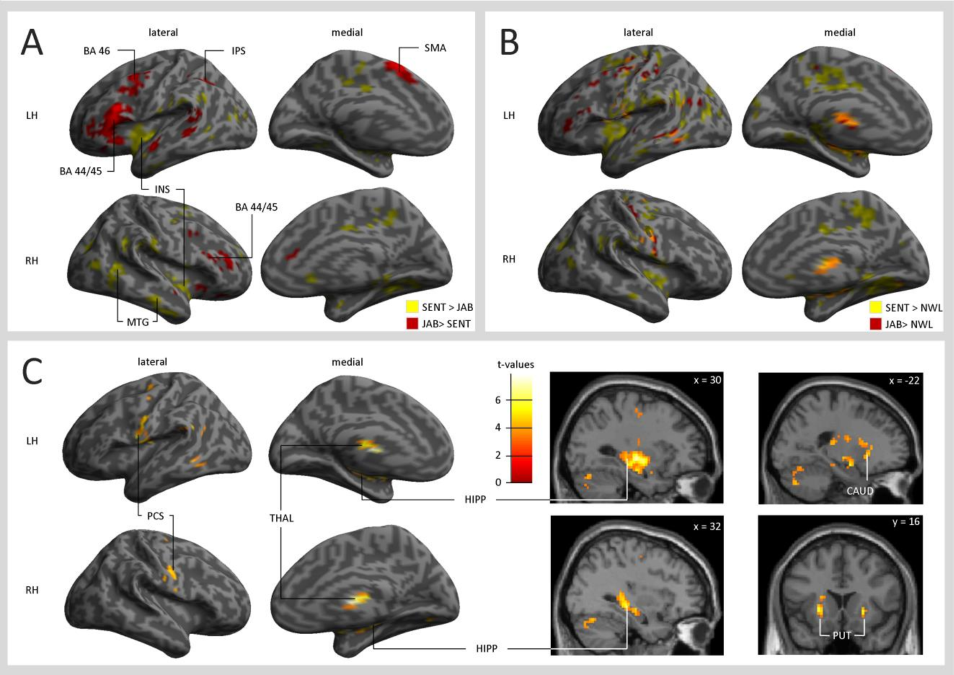


Figure 4-4: FMRI activation pattern. Panel A: T-contrast showing areas that are more strongly engaged in word or word category prediction compared to no prediction (i.e., NWL context), respectively. Panel B: T-contrasts depicting areas that are specifically engaged in either word (i.e., SENT context) or word category prediction (i.e., JAB context). Panel A: Conjunction analysis (SENT > NWL) & (JAB > NWL), indicating the brain regions supporting word category prediction. CAUD, caudate; HIPP, hippocampus; INS, Insula; IPS, intraparietal sulcus; JAB, jabberwocky sentences; LH, left hemisphere; MTG; middle temporal gyrus; NWL, non-word lists; PCS, precentral sulcus; PUT, Putamen; RH, right hemisphere, SENT, normal sentences; SMA, supplementary motor area; THAL, thalamus.

Table 4-1: Activation clusters and increased activation peaks during word vs. word category prediction.

Brain region	**Hemi-sphere**	**Cluster size (voxel)**	**BA**	z_{max}	**MNI coordinates**		
					x	**y**	**z**
SENTENCES > JABBERWOCKY							
Superior frontal sulcus	L	12	8/9	4.67	-18	50	16
	R	13	8/9	3.71	24	50	19
Precentral gyrus	R	13	4	4.45	39	-4	43
Medial temporal lobe/insula	L	337					
Insula	L		-	6.28	-39	-16	-8
Superior temporal gyrus	L		22	5.09	-45	-7	-5
Hippocampus	L		-	4.77	-27	-31	-2

Brain region	**Hemi-sphere**	**Cluster size (voxel)**	**BA**	z_{max}	**MNI coordinates**		
					x	**y**	**z**
Amygdala	L		-	4.73	-21	-1	-14
Middle temporal gyrus	L		20	3.26	-54	-13	-29
Medial temporal lobe/insula/basal ganglia	R	381	13				
Insula			-	5.44	42	-10	-5
Inferior temporal gyrus	R		20	5.28	51	-13	-29
Middle temporal gyrus	R		21	5.16	66	-19	-20
Amygdala	R		-	4.90	39	-4	-26
Thalamus	R		-	4.83	21	-13	-2
MTG / inferior temporal sulcus	R		22	4.77	42	-2	-32
Putamen	R		-	4.23	18	11	-2
Medial anterior STG/rolandic operculum	R		43	3.89	57	8	1
Hippocampus	R		-	3.88	24	-25	-11
Posterior cingulate	L	23	31	3.84	-15	-31	37
Medial temporal lobe	R	177					
Parahippocampal gyrus			20/37	5.20	33	-46	-11
Lingual gyrus	R		19	4.57	18	-58	-5
Hippocampus	R		-	4.25	18	-34	1
Cerebellum	R		-	4.05	12	-40	-8
Parahippocampal gyrus	R		-	3.72	30	-34	-11
Supramarginal gyrus	L	22	40	5.10	-51	-52	31
	R	123	40	5.06	51	-46	28
Middle temporal gyrus (posterior)	L	19	21	4.21	-48	-58	1
	R	117	20	4.84	45	-55	7
Fusiform/lingual gyrus	L	17	37	4.45	-30	-55	-8
Superior occipital cortex	R	131	19	5.50	39	-67	16
Middle occipital cortex	L	26	18	5.34	-39	-79	16
Putamen	L		32	4.13	-18	11	4
Cingulate/precuneus	L / R	179					
Middle cingulate cortex	L		23/24	5.13	-12	-16	34
Middle cingulate cortex	R		23/24	4.41	9	-28	40
Precuneus	R		7	4.16	6	-43	43
Paracentral lobule	L		6	4.15	-3	-22	58
Anterior cingulate cortex	R	14	24	4.58	0	-20	5
Thalamus	R	14	-	4.34	12	-28	7
	L	22	-	5.29	-12	-31	4
Cerebellum	L	46	-	4.99	-3	-40	-20
JABBERWOCKY > SENTENCES							
Inferior frontal gyrus/insula	L	591					
Pars triangularis	L		44/45	7.18	-45	20	19
Inferior frontal gyrus (p. orbitalis)	L		47	4.87	-42	20	-8
Insula/Frontal operculum	L			4.68	-30	20	-5

Brain region	**Hemisphere**	**Cluster size (voxel)**	**BA**	z_{max}	**MNI coordinates**		
					x	**y**	**z**
Orbital sulcus (dividing anterior and posterior portion of the orbital gyrus)	L		46/10	4.54	-42	44	-2
Frontal gyrus	R	129					
Inferior frontal gyrus (p. triangularis)			45	4.95	48	35	16
Middle frontal gyrus	R		46	4.03	33	44	10
Frontal gyrus/insula/basal ganglia	R	93					
Inferior frontal gyrus (p. orbitalis)			47	5.18	33	32	-8
Insula/Frontal operculum	R		-	4.61	39	20	-2
Middle frontal gyrus (anterior), extending into orbital sulcus	R		11/47	4.48	33	50	-11
Putamen	R		-	4.40	30	17	-2
Supplementary motor area	L	243	6	6.44	-6	14	58
Superior medial gyrus	L		6/8	4.59	0	26	40
Inferior frontal gyrus (p.Opercularis)	R	46	44	3.56	42	11	37
Precentral gyrus	L	226	4	6.38	-39	2	49
Superior temporal sulcus	L	58	21	5.72	-51	-7	-14
	L	105	21	4.88	-60	-40	7
	R	16	22/21	4.37	54	-4	-14
Intraparietal sulcus	L	65	39/7	4.99	-24	-49	37
Angular gyrus/intraparietal sulcus			39/7	4.80	-33	-58	37
Anterior cingulate cortex	R	14	24	3.95	15	38	13
Caudate nucleus	R	39	39	3.86	15	-1	22

Table 4-2: Activation clusters and increased activation peaks during prediction - conjunction analysis.

Brain region	Hemisphere	Cluster size (voxel)	BA	z_{max}	MNI coordinates		
					x	y	z
CONJUNCTION ANALYSIS OF (A) SENTENCES - NON-WORD LISTS AND (B) JABBERWOCKY – NON-WORD LISTS							
Superior frontal sulcus	L	20	6/8	3.64	-27	-16	52
	R	12	6	3.69	30	-10	52
Precentral gyrus (premotor cortex)	L	99	6	4.59	-63	-13	7
	R	55	3a	4.12	51	-7	28
Insula	L	12		4.12	-33	-10	19
Posterior inferior temporal sulcus (MTG/ITG)	L	22	21/37	5.02	-48	-46	-8
Posterior middle temporal sulcus	L	13	21	3.92	-42	-58	22
Supramarginal gyrus	L	16	40	3.93	-54	-49	25
Medial temporal lobe	R	196					
Amygdala	R		-	5.64	27	-4	-11
Putamen	R		-	5.34	24	17	-2
Hippocampus	R		-	5.34	33	-28	-5
Medial temporal lobe/basal ganglia	L/R	442					
Putamen	L		-	7.16	-27	-16	-2
Thalamus	L		-	5.48	-24	-28	13
Thalamus	R		-	5.72	0	-10	7
Hippocampus	L		-	5.50	-33	-22	-11
Hippocampus	L		-	3.42	-21	-25	-14
Amygdala	L		-	3.81	-27	2	-20
Thalamus	R	14		3.94	24	-22	16
Caudate nucleus	L	16	-	4.08	-18	14	13
Cerebellum	L	50	-	4.43	-27	-73	-23
	L	34	-	4.73	-18	-76	-35
	R	166	-	6.44	15	-79	-32
Truncus cerebri (Pons)	L	15	-	4.76	-9	-37	-32

4.6 DISCUSSION

Recently, predictive processes have increasingly been accepted as an integral part of language processing; however tackling prediction experimentally requires sophisticated paradigms to dissociate predictive from concurrent sensory processing. The present study firstly provides direct behavioral evidence for the existence and timing of predictive linguistic processes (specifically, syntactic category prediction and word prediction) and secondly the neural substrates underlying prediction processes.

This evidence is based on a newly developed predictive eye gaze reading task which allows capturing predictive processes during sentence comprehension by measuring anticipatory eye gazes during the delayed presentation of the sentence-final word in contexts with variable syntactic and semantic predictability. Critically, participants were not explicitly instructed to predict the upcoming word or to engage in anticipatory eye movements. The presence of coherent semantic and syntactic context in normal sentences as compared to only syntactic context in jabberwocky sentences led to an increase in the speed of anticipatory saccades, demonstrating that linguistic predictions can operate on different types of linguistic information. These findings attest the suitability of the current paradigm to assess the time-course and representational basis of linguistic predictions, thereby providing the foundation for our second aim of exploring of the neural basis of linguistic predictions. This was achieved by using the timing information regarding the predictive process that we gained from eye tracking to inform our fMRI model.

4.6.1 SPECIFIC MECHANISMS FOR SYNTACTIC VS. SEMANTIC PREDICTIONS

The fMRI data revealed different activation patterns for linguistic predictions in normal sentences and jabberwocky sentences based on the differential presence of semantic and/or syntactic cues in the predictive context. For word category predictions as compared to actual word prediction our data demonstrate increased activity in a number of brain regions including left Broca's area (Brodmann Areas 44/45) which has been associated with complex syntax processing (Fiebach et al., 2005; Friederici et al., 2006) and also with increased working memory demands during sentence processing (cf. Grodzinsky & Santi, 2008; Rogalsky, Matchin, & Hickok, 2008). Regarding syntactic predictions, this result is consistent with recent lesion data (Jakuszeit et al., 2013). Additionally, the increased intraparietal sulcus (IPS) activity during word category prediction hints towards engagement of the attention system, as the IPS has been reported to be functionally connected to premotor and cerebellar cortices during serial/temporal order processing with high attentional needs (Majerus et al., 2006). The additional involvement of multiple brain regions despite the fact that fewer sources of information were available to base the decisions on plus slower anticipatory eye gazes and decreased performance in grammaticality judgments clearly indicate that relying exclusively on syntax as in the context of meaningless jabberwocky sentences rendered the word category prediction more difficult than in meaningful sentences. These effects presumably result from the fact that in natural communication jabberwocky sentences do not occur; however, jabberwocky sentences allow to identify those brain systems involved in purely syntactic word category predictions. At a first glance, the increased task difficulty might additionally suggest enhanced working memory maintenance demands; however, we showed earlier that syntactic structure leads to a decrease, not an increase of activation during maintenance of structured language (cf. Bonhage et al., 2014). Thus, we suggest that in the present study, Broca's area supports syntactic prediction rather than verbal maintenance. The recruitment of additional controlled syntactic processes for generating syntactic predictions based on jabberwocky sentences might be necessary to compensate for the lack of semantic context.

The involvement of Broca's area during word category prediction was hypothesized; however, why was Broca's area not also involved in predicting words in simple normal sentences, i.e., in the presence of semantic cues? Although the latter finding is not in line with our original expectations, it is consistent with studies using a word category violation paradigm. Violating word categories in normal sentences did not result in activation in Broca's area, but rather in the frontal operculum (Brauer & Friederici, 2007; Friederici, Ruschemeyer, Hahne, & Fiebach, 2003). Activation in Broca's area was only found for normal sentences under increased attentional processing demands (Friederici, Kotz, Scott, & Obleser, 2010). Thus, Broca's area seems to take action when syntax is the only cue available (present finding), when attentional demands on syntactic processes are high (Friederici et al., 2010), and/or when sentence structure is more complex, e.g., in sentences with non-canonical argument order (Fiebach & Schubotz, 2006; Friederici et al., 2006).

In contrast to jabberwocky sentences, normal sentences allow participants to predict a specific word, thus we expected more predictive engagement of brain areas implicated in (lexical-)semantic processing. Indeed, word as opposed to word category prediction specifically increased activation in supramarginal gyrus, formerly associated with the processing of strong semantic associations (Chou et al., 2006) and creativity tasks (Bechtereva et al., 2004), and in middle temporal gyrus, previously reported for multimodal semantic processing and lexical decision (Fiebach, Friederici, Muller, & von Cramon, 2002; Visser, Jefferies, Embleton, & Ralph, 2012). Note that the activation clusters are larger in the right than left hemisphere; this is remarkable because it diverges from the typical left-lateralization of language. However, the right hemisphere has been suggested to play an integral role in sentence completion when the task requires the maintenance of multiple meanings (Kircher, Brammer, Tous Andreu, Williams, & McGuire, 2001). Our results extend this interpretation by suggesting a role of the right hemisphere in predicting upcoming (lexical-)semantic input.

Additional to areas associated with semantic processing, our data reveal more activity in occipital and fusiform cortex for predictions of specific words. In a series of elegant experiments, Dikker and colleagues were able to show effects of syntax and semantics in visual cortex on a time scale below conscious perception (Dikker & Pylkkanen, 2011; Dikker et al., 2010; Dikker et al., 2009). The authors argue that the activation of perceptual areas might indicate that participants expect a specific word form. In line with this, we speculate that when our participants predicted the sentence-final words, they may in fact have anticipated its specific visual form.

4.6.2 PREDICTION OF WORDS AND WORD CATEGORIES: GENERAL BRAIN SYSTEMS UNDERLYING LINGUISTIC PREDICTIONS

Both normal and jabberwocky sentences share the property of syntactic phrase structure based on the availability of function words and morphosyntactic information and the availability of word category information of the target word. Thus, a conjunction analysis was employed to reveal word category-based syntactic prediction shared by both conditions, revealing engagement of subcortical areas that have been associated with language processing recently, i.e., thalamus (Wahl et al., 2008) and caudate nucleus (Ali, Green, Kherif, Devlin, & Price, 2010; Crinion et al., 2006; Price, 2010). As noted above, the fact that Broca's area did not show such a conjunction effect likely results from the rather simple sentence structures used in the present study and from lexical-semantic support in the sentence condition.

Due to the sequential character of the linguistic input, we additionally expected that areas supporting sequence processing contribute to linguistic predictions. Indeed, the cerebellar involvement is in line with its sequence detection and prediction capacity (Molinari et al., 2008). Additionally, the ventral premotor cortex was activated - an area that has been associated with the mapping of sequential input onto structural linguistic templates (Fiebach & Schubotz, 2006) and the processing of linguistic dependencies according to local phrase structure (Opitz & Kotz, 2012). Prominent activation was also found in bilateral hippocampi, which have been reported for linguistic processing before (mostly in patient studies, cf. Duff & Brown-Schmidt, 2012; Meyer et al., 2005; Tracy & B. Boswell, 2008), but also for predictive processing: Relying on its information storage and binding functions as well as its coding for successive neuronal firing patterns over time (cf. Schiffer et al., 2012), the hippocampus might be able to match anticipated sequences of cortical activation patterns (Diba & Buzsaki, 2007) with the actual perceptual input, enabling the computation of prediction errors (e.g. J. Chen et al., 2013). Both prediction and prediction error detection are possible reasons for the hippocampal and cerebellar engagement in our paradigm: Although predicting the missing element seems plausible, an irregular temporary omission of an expected element might also induce a mismatch between expectation and actual input (i.e., a prediction error). Taken together, our neurophysiological results support the validity of the predictive coding model (de-Wit et al., 2010; Friston & Kiebel, 2009; Huang & Rao, 2011; cf. Rao & Ballard, 1999) for the linguistic domain: Areas known to be involved in processing linguistic and sequential information were also involved in predicting upcoming elements of linguistic sequences.

4.6.3 CONCLUSION

The present study provides direct neurobehavioral evidence for predictive linguistic processes based on a novel predictive eye gaze reading task, which allows the temporal specification of linguistic anticipations in fMRI data. Word category (i.e., syntactic) predictions were associated with activation of inferior frontal cortices attributed to syntactic processing, while specific activations for word predictions were mainly found in temporal regions commonly implicated in (lexical-) semantic as well as visual processing. Moreover, both types of predictions elicited activation in a domain-general system for sequential predictive processing, i.e., hippocampus, basal ganglia and thalamus, as well as premotor cortex. In line with the assumptions of predictive coding, domain-general sequence processing systems interact with cortical language systems during predictive processing in the domain of linguistics.

5 GENERAL DISCUSSION

Verbal communication requires online processing of current information while simultaneously bearing in mind previous conversation contents and connecting the perceived information to our existing world knowledge. Memorizing sentences has been proven to differ substantially from memorizing unconnected words (cf. Baddeley et al., 2009; Brener, 1940; Jefferies et al., 2004; Potter & Lombardi, 1990, 1998; Rummer, 2003): Sentences allow humans to recall a significantly larger number of words compared to word lists. Although there has been some effort to explain this so-called 'sentence superiority effect', the distinct influence of sentence structure on the encoding versus the maintenance of items had not been disentangled yet. In order to fill this gap, the first part of the present thesis focused on investigating those characteristics of language that help to memorize sentences and their neural underpinnings, demonstrating that sentences benefit from a structurally and semantically enriched encoding process that subsequently reduces the demands on working memory maintenance. A short result summary and a detailed discussion are provided in section 5.1.

However, the current input is not only stored in working memory; additionally it is assumed that it is linked online to preexisting memory contents and, in combination with the latter, used to generate predictions about future events. Therefore, the second part of the present thesis is concerned with predictions in the linguistic domain. Given the huge amount of sensory input at any point in time, current models of neurophysiological information processing suggest that the speed of information processing can be enhanced considerably by the means of predictive coding (cf. de-Wit et al., 2010; Friston & Kiebel, 2009; Rao & Ballard, 1999). The predictive coding framework proposes that we store and constantly update internal models of the world in our memory that help us to understand new input and enable us to *predict* likely upcoming input based on earlier analogous[9] experiences (Bar, 2007, 2009). This general rationale might apply to language processing: Many years of perceiving and producing language result in an enormous body of linguistic knowledge. Some authors have argued that our linguistic experience might enable us to anticipate future linguistic input with respect to various aspects of language (e.g., syntax, semantics, perceptual features; cf. Dikker & Pylkkanen, 2011; Dikker et al., 2010; Dikker et al., 2009; Federmeier et al., 2007; Lau et al., 2006; Levy, 2008; Pickering & Garrod, 2013; Smith & Levy, 2013). As predictive processing

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[9] Moshe Bar describes the process of generating an analogy as seeking for correspondence between currently processed, novel input and previously experienced, already existing representations in memory (Bar, 2007). The term "analogy" will be used accordingly throughout the present thesis.

in language usually happens simultaneously with ongoing perceptual processing, isolating the anticipation of future linguistic content and extracting its neural substrate constitutes the second major focus of the present thesis; section 5.2 summarizes the results of the combined eye tracking and fMRI measurements and discusses their implications with respect to current scientific concepts regarding the role of prediction in language processing. Finally, section 5.3 will integrate the neurophysiological evidence from memory and prediction processes and highlight their commonalities.

5.1 MEMORIZING SENTENCES – BENEFITS OF SYNTACTIC STRUCTURE

Sentence structure improves working memory performance for words: When asked to memorize word lists over a short time interval, adults only recall approximately 5-6 words correctly, whereas the number of properly memorized words can be increased significantly in a sentence (i.e., the 'sentence superiority effect'; cf. Baddeley et al., 2009; Brener, 1940; Jefferies et al., 2004; Potter & Lombardi, 1990, 1998; Rummer, 2003). But which of the consecutive stages of the working memory process – encoding, maintenance, and/or retrieval (Chein & Fiez, 2001) – is influenced by sentence structure? Previous literature has tried to account for the sentence superiority effect by proposing different encoding (Baddeley et al., 2009; Jefferies et al., 2004; Potter & Lombardi, 1990, 1998) and retrieval (Potter & Lombardi, 1990, 1998; Schweppe & Rummer, 2007) mechanisms, neglecting to differentiate between the influences of sentence structure on the encoding of words versus its effect on the maintenance of sentences. For this reason, the memory study described in chapter 0 aimed at (a) disentangling the effects of sentence structure on encoding and maintenance of words and (b) investigating their neurophysiological substrate. Moreover, as effects of sentence structure should be differentiated from working memory load effects, (c) both sentence structure and working memory load were varied systematically. Finally, the availability of sentence structure during encoding might influence whether or not participants make use of rehearsal strategies (i.e., the overt or covert repetition to memoranda during the maintenance phase), thus (d) a last manipulation was added to the experimental design: Rehearsal was prevented in half of the experimental trials by forcing the participants to utter meaningless syllable sequences during maintenance (i.e., Articulatory Suppression; see Hanley & Thomas, 1984; Murray, 1968).

Based on prior research regarding the sentence superiority effect (Baddeley et al., 2009; Brener, 1940; Jefferies et al., 2004; Potter & Lombardi, 1990, 1998; Rummer, 2003), behavioral performance in the present working memory task was expected to increase in items with sentence structure compared to ungrammatical word sequences, in items with low compared to high load, and in items where rehearsal was possible (i.e., without Articulatory Suppression). All three effects were confirmed by the present results. Furthermore, sentence structure was expected to decrease the detrimental effects of larger item sets (which usually increase the demands on the working memory system) and Articulatory Suppression. This assumption was confirmed in terms of accuracy: When sentence structure was available, larger item sets and Articulatory Suppression did not lead to lower performance, which was the case in ungrammatical items. Thus, the sentence superiority effect was reliably replicated and the behavioral results indicate that sentence structure indeed is used to cope with larger amounts of input (i.e., high working memory load) and with circumstances when rehearsal as a memorization strategy is not available. The sentence superiority under non-rehearsal conditions was in line with Baddeley and colleagues (Baddeley et al., 2009), who demonstrated that the sentence superiority effect continues to exist under conditions comprising Articulatory Suppression. Taken together, at a behavioral level the hypotheses were confirmed: The paradigm successfully elicited the sentence superiority effect and thus allows investigating the influences of SST on working memory load and Articulatory Suppression in terms of their underlying brain processes. The following three sections will summarize the neurophysiological results of the present working memory study, discuss their implications for existing memory models, and ultimately provide a critical reflection on the conducted experiments.

5.1.1 NEURAL SUBSTRATES OF THE SENTENCE SUPERIORITY EFFECT

On the neurophysiological level, the working memory study detailed in chapter 0 was the first to disentangle the neural substrates of encoding and maintaining words in the presence and absence of sentence structure: A stronger engagement of the semantic system and the hippocampus during sentence perception pointed to a semantically and structurally enriched encoding process, which subsequently led to a less demanding maintenance of words (as indicated by decreased activity in brain regions supporting working memory maintenance and attention).

A similar general pattern of increased followed by decreased neurophysiological engagement has been reported by two studies investigating memory processes for structured versus unstructured spatial and numerical sequences (Bor et al., 2004b; Bor et al., 2003). The authors described activation increases during encoding for structured items, followed by decreased activity during item maintenance; this result pattern was argued to reflect lower demands on working memory maintenance due to an enriched encoding process, an interpretation which is in line with the present results.

In addition to estimating the general effects of sentence structure during encoding and maintenance, the present study was designed to disentangle the influences of sentence structure from effects of increased working memory load and Articulatory Suppression and investigate their interactions. The resulting complex fMRI result pattern of the encoding and maintenance phase will be summarized and discussed in the following two sections, respectively. Afterwards, the results will be related to established theories of working memory (cf. section 5.1.2).

5.1.1.1 ENCODING SENTENCES

The present fMRI study demonstrated that during encoding, sentence structure led to enhanced activity in widely distributed brain regions: Both cortical areas (such as left BA 45/47, dorsomedial PFC as well as middle temporal and inferior parietal gyri) and subcortical areas such as the hippocampus/parahippocampus revealed stronger activity for sentences than ungrammatical word sequences. Interestingly, on the cortical level, the activation pattern strongly resembled the network proposed to support semantic processing (see Binder, Zahn, & Mertig, 2001 for an extensive review of neuroimaging data). In addition, the hippocampal/parahippocampal activity has to be explained: The hippocampus codes for structured sequences across different domains (such as e.g. spatial, event, or odor sequences; cf. Buckner, 2010; Fortin, Agster, & Eichenbaum, 2002; Kumaran & Maguire, 2006; Lisman & Redish, 2009), has been related to both memory and prediction (see e.g. Buckner, 2010; Lisman & Redish, 2009; Squire, 1992) and has been shown to be sensitive to syntactic structure in word sequences as well (cf. Meyer et al., 2005). In terms of working memory, the hippocampus has been associated with the episodic buffer (i.e., an interface between short- and long-term memory proposed by the multi-component model by Baddeley; a detailed discussion is provided in section 5.1.2.1), which has been argued to support the chunking of single elements into larger units of information (Baddeley et al., 2009). Additionally, in the reverse contrast, more activity for ungrammatical sequences than for sentences was found in parts of the fronto-parietal attention network (Majerus et al., 2006; Markett et al., 2014), suggesting – unsurprisingly – a more effortful processing of ungrammatical word sequences.

Overall, the fMRI pattern indicates an enriched encoding of sentences, which automatically trigger an engagement of the semantic network and general chunking processes. The presence of semantic processes might be interpreted in line with the conceptual regeneration hypothesis by Potter and Lombardi (Potter & Lombardi, 1990, 1998), who suggest that sentences are memorized and recalled based on their meaning; the authors argue that the encoded linguistic information (i.e., syntactic structure and semantic information) serves as a prime (‘primes’ can be translated to ‘pre-activations’ in neurophysiological terminology) during retrieval; based on these linguistic primes, the sentence is re-generated at recall. This assumption is supported by the present semantic network activation for sentences during encoding; however, if Potter and Lombardi are correct, than brain regions supporting syntactic structure processing should also be activated. One of the most established regions associated with syntax processing is Broca’s area (BA 44/45, e.g. Friederici et al., 2006; Makuuchi et al., 2009; Santi & Grodzinsky, 2010), thus one might have expected activity in Broca’s area for sentence processing during encoding, which was not found in the present study. However, the missing engagement of Broca’s area might be explained by the characteristics of the stimulus material: In the aforementioned studies, sentences with higher syntactic complexity were compared to simple sentences, demonstrating increased activity in Broca’s area for more complex sentences. As the present paradigm used simple sentence structures only, the necessity of support by Broca’s area might be reduced. In simple sentences (as compared to word lists), syntactic features have been reported to be processed in left anterior temporal regions instead (Humphries et al., 2006; Kaan & Swaab, 2002; Stowe et al., 1998; Vandenberghe et al., 2002), which is in line with the present results.

To sum up, the present data suggest that the participants use sentence structure to automatically chunk all words of a sentence into a larger, meaningful unit during encoding. Moreover, the enhanced activity of brain systems involved in semantic and syntactic processing during sentence encoding is in line with the assumptions of the conceptual regeneration hypothesis by Potter and Lombardi (Potter & Lombardi, 1990, 1998), who argue that semantic and linguistic primes are generated during encoding.

5.1.1.2 MAINTAINING SENTENCES

In two consecutive studies (Bor et al., 2004b; Bor et al., 2003), Bor and colleagues were able to demonstrate that structured sequences of numbers or spatial locations lead to increased encoding and decreased maintenance activity. Hypothesizing that sentence structure leads to a comparable effect in the linguistic domain, sentences maintenance was expected to be reflected in activation decreases compared to maintaining ungrammatical word sequences. Indeed, the neurophysiological activation pattern in the present study confirmed this hypothesis: The lower activity level in areas generally associated with maintenance of items during delay phases (i.e., right BA 46; Curtis & D'Esposito, 2003), with phonological storage (i.e., left inferior parietal lobule; Awh et al., 1996), and in more general terms with cognitive control (i.e, bilateral premotor areas, SMA, right frontal gyrus, intraparietal sulcus; Kubler et al.,

2006) while maintaining sentences are in line with the prior expectations. In short, the present neurophysiological data underscore that maintaining sentences is less demanding than retaining ungrammatical word sequences.

Given that the present results are in line with previous literature on working memory processes in- and outside the domain of language, a necessary next step is to discuss potential new insights relevant for selected models of memory in the following section.

5.1.2 IMPLICATIONS OF ENRICHED ENCODING AND FACILITATED MAINTENANCE OF SENTENCES FOR ESTABLISHED MODELS OF WORKING MEMORY

The two-fold activation pattern of encoding and maintaining syntactically structured items provides strong evidence for a qualitatively distinct memorization process in language, suggesting syntactically enriched encoding processes for sentences that lower the overall cognitive effort, the working memory load, and the need for rehearsal during maintenance. The following sections 5.1.2.1 - 5.1.2.3 evaluate the proposals regarding working memory for sentences postulated by the multiple component model of working memory (Baddeley, 2000; Baddeley et al., 2009; Baddeley & Logie, 1999) and discuss propositions brought forward by process models of working memory (Cowan, 1999; Zhou et al., 2007) and the concept of relational memory (Cohen et al., 1997; Konkel & Cohen, 2009; Konkel et al., 2008) in the light of the present results.

5.1.2.1 MULTIPLE COMPONENT MODEL

As described in the general introduction, the multiple component model of working memory (Baddeley, 2000; Baddeley et al., 2010; Baddeley et al., 2009; Baddeley & Logie, 1999) consists of four components: Two short-term buffers (visual and phonological) maintaining the latest input in the respective domain, a central executive (i.e., a limited-capacity attentional system), and an episodic buffer which interfaces and integrates long-term and short-term memory contents. Baddeley and colleagues (2009) systematically investigated the sentence superiority effect and concluded that sentence structure triggers chunking of words into larger meaningful units. Chunking – a process that expands working memory capacities by binding multiple single items into a combined information "chunk" – is considered to be an automatic encoding process that relies on the episodic buffer (cf. McNulty, 1966; Miller, 1956; Tulving & Patkau, 1962). As the episodic buffer in turn is proposed to be supported by hippocampus/parahippocampus (cf. Berlingeri et al., 2008; Luck et al., 2010; Rudner, Fransson, Ingvar, Nyberg, & Ronnberg, 2007; Mary Rudner & Jerker Ronnberg, 2008), the multiple component model would predict that the hippocampus is engaged during encoding because of an ongoing chunking process. This claim is supported by the present data, as encoding of sentences (compared to ungrammatical word sequences) indeed led to an increase in hippocampal activity. However, the activation of the semantic network during sentence encoding in the present study suggests that generating a meaningful chunk might additionally rely on the semantic processing resources.

Combining encoding and maintenance results, the present study indeed supports the claims of the multiple component model: Linguistically structured word sequences (i.e., sentences) trigger the binding of single words into larger, meaningful units during encoding. Functional MRI data propose that the structurally enriched encoding leads to a reduced effort in maintaining sentences and helps participants to cope with larger numbers of items as well as with conditions in which rehearsal is prohibited.

5.1.2.2 PROCESS MODELS

In process models of working memory such as the embedded processing model (Cowan, 1999) or the active memory model (Zhou et al., 2007), working memory maintenance is conceptualized as sustained activity of task-relevant domain-specific representations in long term memory: Items stay accessible for retrieval when they are attended to. In his embedded processing model, Cowan proposes that working memory consists of two levels: the currently activated part of long-term memory and an even smaller subset of memory representations in the ‘focus of attention’, a limited-capacity subset of activated items that is accessible for selection (consisting of 3-5 information chunks, cf. Cowan, 2010). Cowan’s model has been extended by Oberauer and colleagues, who propose a third embedded level – the narrow focus of attention that selects one information chunk at a time (Oberauer, 2002; Oberauer & Hein, 2012). In terms of neuronal activity, Oberauer and colleagues found that holding task-relevant representations in the broad focus of attention was reflected in sustained activation during maintenance (Lewis-Peacock, Drysdale, Oberauer, & Postle, 2012); a similar observation was made in studies investigating the beneficial effects of word-level semantic (Fiebach et al., 2007) and lexical information (Fiebach et al., 2006) on working memory performance, who demonstrated engagement of language-related areas during working memory maintenance of words.

In consequence, in the present study it was hypothesized that maintaining items with sentence structure should rely on sustained activity in brain regions supporting all aspects of linguistic processing (such as e.g. semantics, syntax, lexical access) starting at the encoding and persevering the maintenance interval. Our results only partly support this notion: Although encoding sentences (compared to ungrammatical word sequences) indeed increased the activation in language-related areas, this activity pattern was not sustained during the maintenance phase. Instead, the stronger activation of language areas during encoding was followed by substantial activation decreases in cognitive control/WM maintenance regions during maintenance.

However, as our primary analysis explicitly focused on the *difference* between sentences and ungrammatical word sequences during encoding and maintenance, the two conditions were contrasted directly for each phase. This implies that the different activation pattern in the contrast "sentences > ungrammatical word sequences" during encoding compared to the (de-)activation pattern during maintenance could in principle be due to changes in the neural activity in response to ungrammatical word sequences only. In contrast, investigating sentence encoding and maintenance independent of the ungrammatical word sequences, might reveal areas activated during both phases.

Thus, an additional contrast was calculated to search for neurophysiological evidence for the embedded processing model in the language domain: In a first step, two baseline contrasts discovering all brain regions supporting encoding and/or maintenance of sentences were estimated. Afterwards, the activity pattern from maintaining sentences (without Articulatory Suppression) was masked by the activation map for sentence encoding (again in conditions without Articulatory Suppression)[10], thereby attempting to extract brain regions that display activation during both encoding and maintenance. However, the masked contrast did not reveal any significantly activated voxels (even when using a decreased significance threshold of $p < .001$, uncorrected for multiple comparisons). Thus, based on the present results, we cannot verify sustained activity to be the driving force of working memory for sentences.

5.1.2.3 RELATIONAL MEMORY

A third theoretical approach that may also contribute to the understanding of the sentence superiority effect proposes a "relational memory" (Cohen et al., 1997; Cohen et al., 1999; Konkel & Cohen, 2009; Konkel et al., 2008), pointing out that multiple items are not only encoded as such (i.e., 'item memory'), but that their interrelation is stored additionally (i.e., 'relational memory'). Although Cohen and colleagues do not specifically address verbal working memory, the concept of a 'relational memory' aligns well with the proposal that in sentences

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[10] Conditions containing Articulatory Suppression were not included in the contrast, because Articulatory Suppression was only performed during the maintenance phase. Therefore e. g. areas involved in inner and overt articulation might be active during encoding and maintenance, but for different reasons: During encoding, they might support inner co-articulation of the presented word sequences, whereas during maintenance they are engaged because of overt articulation demands inflicted by Articulatory Suppression.

not only single words are stored, but the sentence structure helps connecting single words to generate a sentence-level meaning. Cohen and colleagues (Konkel & Cohen, 2009; Konkel et al., 2008) suggest that the binding processes underlying relational memory are realized in the hippocampus. This proposal is supported by the present fMRI results, which indeed demonstrate large clusters of activation in bilateral hippocampi/parahippocampi during sentence encoding. However, as the hippocampal engagement in the current study was accompanied by activation of a language system previously reported for semantic processing, the results suggest that binding processes are supported by domain-specific neural networks as well. As, the ungrammatical condition in the present study comprised the exact same words as the sentence condition, the stronger engagement of the semantic/simple syntax network in sentences as compared to ungrammatical word sequences cannot be explained as simply reflecting the access to lexical items in the mental lexicon. Instead, the present results suggest that words in sentence structure lead to an automatic generation of a combined message-level meaning. Therefore, the activation of the semantic network probably reflects domain-specific support (additional to the presumably domain-general hippocampal engagement) for combinatorial binding processes in relational memory, resulting in a memory representation of a meaningful information unit rather than item (i.e., single element) memory.

5.1.3 CRITICAL REFLECTIONS

The present study focused on the first two stages of the working memory process, as disentangling encoding and maintenance processes based on behavioral experiments alone is fairly challenging and does not reveal the neural systems underlying the sentence superiority effect. However, instead of focusing on the distinction between encoding and maintenance, some researchers have claimed a fundamentally different recall process for sentences compared to ungrammatical word lists (Potter & Lombardi, 1990, 1998; Rummer & Engelkamp, 2001). Thus examining the neurophysiological response patterns at recall might be a necessary next step in gathering evidence for distinct working memory processes during retention of sentences. At a first glance, the question arises why the recall phase was not subject of investigation in the present study? The reason was that the present working memory task not only required that participants recalled word sequences in their original order, but additionally asked them to decide whether one word of the sequence was presented before another word in the original sequence; therefore the processes underlying sequence recall and judgment of serial position congruency are inseparable. Hence, investigating the recall of sentences would require a slightly changed working memory task that – importantly – nonetheless assures that the participants do not try to reorder the words of the ungrammatical condition into a grammatically valid sequence.

As stated in the beginning of the general discussion, the brain is presently conceptualized as an active rather than passive information processing organ: Instead of passively waiting for perceptual information from the environment, the brain is proposed to estimate probable next perceptions based on its internal models of the world (Arnal & Giraud, 2012; de-Wit et al., 2010; Friston & Kiebel, 2009; Huang & Rao, 2011; Rao & Ballard, 1999). These top-down expectations are constantly generated based on analogous events the person has experienced before (Bar, 2007, 2009; Bubic, von Cramon, & Schubotz, 2010) and are thought to facilitate bottom-up perceptual processing and cognition because relevant memory representations are pre-sensitized (Bar et al., 2006): For example, when you are entering an office, based on prior experiences with offices you will expect to see a desk and pre-activate the concept 'desk' (as well as other office-related concepts such as 'chair' or 'computer'). In consequence actually seeing the desk leads to comparably low extra-activation, whereas seeing a motor bike would constitute a prediction error and lead to increased cognitive processing. However, as first evidence supporting the predictive coding framework is based on experiments investigating non-linguistic stimuli (such as e.g. Alink, Schwiedrzik, Kohler, Singer, & Muckli, 2010; den Ouden, Kok, & de Lange, 2012), the question remains unresolved whether or not the concept translates to the higher-level cognitive domain of language.

Current neurolinguistic research indeed focuses on the potential role of linguistic predictions in communication (Brunelliere, 2011; Dikker & Pylkkanen, 2011; Dikker et al., 2010; Dikker et al., 2009; Federmeier et al., 2010; Jakuszeit et al., 2013; Lau et al., 2006; Levy, 2008; Pickering & Garrod, 2013; Sohoglu et al., 2012; Van Petten & Luka, 2012). A recent theory by Levy (2008; 2013) formalizes the idea that the "surprisal" (which is conceptually equivalent to 'prediction error'; cf. Schwartenbeck et al., 2013) of the brain regarding an incoming word is reduced with increasing constraints provided by the preceding linguistic context. For instance, over the course of a sentence, the more words have been presented, the less semantic and syntactic options are available for the remaining words, thus the upcoming words become more predictable (and less surprising). As predictive processes might be a valuable component of linguistic processing, it should be pointed out that investigating predictions remains an experimental challenge: How can the researcher be certain that (and when) a participant predicted a specific item?

Most of neurolinguistic research regarding prediction relies on expectation violation paradigms where the perceptual input by definition differs between the correct and the violation condition (see e.g. Federmeier et al., 2007); thus on the neurophysiological level, linguistic predictions cannot be decisively separated from ongoing sensory processing. Therefore, the first part of the present investigation was concerned with creating a paradigm that allows to discriminate prediction and ongoing perception, the so-called "predictive eye gaze reading task". In this task, participants were presented with word sequences such as "Der Reiter wollte das wilde Pferd ohne Sattel --- reiten/*The rider wanted the wild horse without saddle --- to ride (literal translation)*". The first seven words were presented one by one without pauses in the center of the screen, whereas the final target word of the sequence (i.e., either a verb or a noun) was delayed by approximately 5 seconds and presented at a different location on the screen, depending on its word category (i.e., verbs always in the upper right corner, nouns always in the lower right corner; detailed descriptions and illustrations of the paradigm are available in sections 2.4.2, 2.4.3 and 4.3). As the participants were informed and trained to associate the target word categories with their respective screen locations prior to the experiment, predictions regarding the word category of the target word were hypothesized to be reflected in anticipatory eye movements during the delay into the corner where the participants expected the grammatically correct continuation of the sequence to appear. For instance, in the example sentence "Der Reiter wollte das wilde Pferd ohne Sattel/*The rider wanted the wild horse without saddle"*, the participants were expected to predict the verb "reiten/to ride", leading them to redirect their gaze into the upper right corner of the screen already before the actual target was presented. The results of the pilot study (section 2.4.2.2) and the fMRI experiment (see chapter 4) confirmed that participants indeed displayed anticipatory eye movements regarding the syntactic word category whenever the respective cues were available in the preceding word sequence (the same holds true for the semantic prediction version of the experiment described in section 2.4.3.2). Given that the paradigm successfully triggered linguistic predictions as indicated by anticipatory eye movement, the timing of the anticipatory eye movement was used to tackle the neurophysiological substrate of the predictive processes in the fMRI model. Bringing together eye tracking and fMRI data in one analysis revealed prediction-related brain activation during the delay phase of each trial, specifically during a period where participants *did not* perceptually process any linguistic material, but only a light grey screen with dark grey boxes indicating the possible word locations. The following section will shortly summarize the neurophysiological results and link them to previous research.

5.2.1 NEUROPHYSIOLOGICAL SUBSTRATES OF LINGUISTIC PREDICTIONS

In the syntactic prediction study described in chapter 4, predictions of specific words (i.e., in the context of normal sentences) were compared to purely syntactic word category predictions in meaningless jabberwocky sentences and to a baseline condition without cues for prediction (i.e., non-word lists). Functional MRI analyses indicated that predicting a specific word (in comparison to pure word category predictions) was supported by brain regions commonly implicated in semantic processing (such as e.g. middle temporal gyrus, supramarginal gyrus, and insula/frontal operculum; for an extensive review see Binder et al., 2009) as well as visual processing. As low-level visual anticipations of word forms in sentence comprehension have been proposed before (Dikker & Pylkkanen, 2011; Dikker et al., 2010; Dikker et al., 2009), the activity in the visual cortex is probably due to more precise expectations regarding the specific target word, which was not possible to predict in the context of meaningless jabberwocky sentences or non-word lists.

In the absence of semantic cues (i.e., in the context of jabberwocky sentences), anticipatory eye movements revealed that participants were still able to predict the potential word category of the target word. Compared to specific word predictions, both behavioral and fMRI measures indicated a more effortful processing for word category predictions based on syntactic cues only: Behavioral performance in the grammatical judgment task dropped significantly, anticipatory eye gazes were slowed down, and apart from enhanced brain activity going back to syntactic processing in Broca's area (Friederici, 2002; cf. Grodzinsky & Santi, 2008), activation of the fronto-parietal attention network (cf. Majerus et al., 2006) also pointed towards a less automatic process. As jabberwocky sentences do not occur in everyday life, this general increase in task difficulty is not surprising; however, on the neurophysiological level one might have expected Broca's area not only to be involved in word category predictions but also in the prediction of specific words in the sentence context, which was not observed in the present data (i.e., contrast sentences > non-word lists).

Although not exactly in line with our prior hypothesis, lacking activation of Broca's area is consistent with a range of studies investigating word category violations in sentences with simple syntactic structure: Word category violations in normal sentences led to activity in the frontal operculum (which was also found in the present study) rather than in Broca's area (Brauer & Friederici, 2007; Friederici et al., 2003). Thus, Broca's area seems to be utilized when only syntactic cues are available (as indicated by the present findings), when participants process syntactically complex sentences (Fiebach & Schubotz, 2006; Friederici et al., 2006), as well as for language processing under high attentional demands (Friederici et al., 2010).

Both normal sentences and meaningless jabberwocky sentences shared the possibility to predict the word category of the target word. A conjunction analysis revealed shared prediction-related activity in areas that have been associated with syntactic processing (i.e., thalamus and caudate; see Crinion et al., 2006; Price, 2010; Wahl et al., 2008), for matching sequences to structural (syntactic) templates (i.e., premotor cortex; cf. Fiebach & Schubotz, 2006) and for sequence processing across domains (hippocampus and cerebellum; cf. Buckner, 2010; Kumaran & Maguire, 2006; Lisman & Redish, 2009; Molinari et al., 2008; Tubridy & Davachi, 2011).

In sum, the pattern of fMRI results might be considered as new evidence for the proposals brought forward by the predictive coding framework: Those areas commonly reported to support processing of linguistic and sequential information are also involved in generating the respective predictions. Additionally, the present results suggest that when the number of linguistic constraints becomes large enough to predict a specific word, the brain even anticipates the upcoming visual sensory input (as indicated by visual cortex pre-activation).

Although interpreting the present results in the light of the general framework of predictive coding is a valid approach, the present results should also be related to recent findings from prediction studies in the linguistic domain. Over recent years, the potential benefits of predictive processes in language have gained substantial interest in neurolinguistic research. As human adults are in possession of a tremendous linguistic knowledge, this internal knowledge potentially could be used to generate linguistic predictions on all levels of the processing hierarchy: from conceptual predictions regarding probable semantic input or anticipations regarding upcoming word classes down to the very specific prediction of a perceptual input.

Starting with predictions based on semantic context, remember that semantic concepts are extensively interrelated, thus activating one concept (such as e.g. “bathroom”) might automatically co-activate related concepts (such as e.g. “basin”, “shower” etc.). DeLong and colleagues for example were able to demonstrate neuronal pre-activation that was positively correlated with the cloze probability of the target word in a sentence (DeLong, Urbach, & Kutas, 2005): The more precisely the participants could predict a specific noun, the more pre-activation for the matching article preceding the noun (i.e., ‘a’ versus ‘an’) was demonstrated, followed by a smaller N400 effect (i.e., an ERP component commonly related to semantic processing). In short, the response of the brain to a semantic violation was dependent on the predictability of the word given the sentence context. This result was in line with a study by Federmeier and colleagues (2007), who also reported that the expectancy of a word modulated the N400. Thus semantic expectancy (i.e., semantic prediction) seems to affect the processing of consecutive words. The results of the present study support these findings by demonstrating prediction-related semantic network activation in the brain when participants were provided with a constraining sentence context that enabled them to predict a specific word rather than only a word category.

However, as language not only possesses a semantic, but also a structural syntactic aspect, another line of research has focused on a potential priming effect of words/morphemes in a grammatical order for grammatically valid subsequent words/morphemes (cf. Brunelliere, 2011; Hasting, Kotz, & Friederici, 2007; Jakuszeit et al., 2013; Lau et al., 2006; Pulvermüller & Shtyrov, 2003). These studies reported ERP effects as early as 100-200 msec after a syntactic violation, which is close to the time range of perceptual processing. To account for the speed of this higher-level cognitive process, Pulvermüller and Shtyrov proposed a sequence detector, a "neuronal ensemble, which specifically responds to a defined sequence of elementary sensory events (Kleene, 1956), but not to the same events appearing in a different order" (Pulvermüller & Shtyrov, 2003; p. 160). The basic idea of the sequence detector is that in a sequence A-B-C-D-E the perception of element A is enough to prime B-C-D-E in an automatic, fast manner. The present results are in line with this assumption, as both word and word category prediction were supported by areas that have been reported for sequence processing within (i.e., premotor cortex; cf. Fiebach & Schubotz, 2006; Opitz & Kotz, 2012) and outside (i.e., hippocampus and cerebellum; cf. Buckner, 2010; Kumaran & Maguire, 2006; Lisman & Redish, 2009; Molinari et al., 2008; Tubridy & Davachi, 2011) the neurolinguistic domain.

Despite the growing evidence for predictive processes in language and their potential explanation capacities, contemporary neurolinguistic models such as the syntax-first model by Friederici (2002), the MUC (memory, unification, control) model by Hagoort (2005b) or the extended argument dependency model by Bornkessel and Schlesewsky (2006) do not yet specify a role of prediction in language comprehension or production. One recent model implicating predictive processes in communication was brought forward by Pickering and Garrod (2013) and will be detailed in the following section.

5.2.1.1 AN INTEGRATIVE FRAMEWORK FOR LANGUAGE COMPREHENSION AND PRODUCTION

In an attempt to account for the rapidity of linguistic processes and the fluency of dialogues, Pickering and Garrod (2013) suggest that prediction plays a central role in language production, comprehension, and dialogue: Based on research in action (and action perception), dialogue partners are proposed to use forward models in order to predict not only their own, but also the other speakers upcoming utterances. In Pickering's conception, the prediction of the speaker's unfolding utterance is achieved via covert imitation of the speaker by the listener, which leads to an anticipation of the future output of the speaker based on the internal models of the listener. Furthermore, the model assumes that prediction occurs on three linguistic levels: Semantics, syntax, and phonology (anticipation of visual form in reading is discussed as well).

The present study did not investigate a dialogue between conversation partners, but rather visual processing of unrelated single sentences; nevertheless, predictive processes were evidenced. Moreover, in line with the proposal of the integrative framework, the prediction was reflected in engagement of brain regions associated with different aspects of linguistic processing, such as areas supporting simple syntax and semantics as well as involvement of the visual cortex when the prediction of a specific word was possible. However, the present findings deviate from the integrative framework in two respects: First, in addition to those language processing areas suggested by Pickering's model, the present study demonstrated that predicting a word category elicited activation in areas associated with sequence processing (i.e., ventral premotor cortex, cerebellum, and hippocampus; for a full discussion, the reader is referred to section 4.7.1). This activation pattern suggests that predictive processing in language might not solely rely on classical cortical language regions, but additionally draw upon domain-general brain systems when covertly continuing a syntactically structured word sequence.

Moreover, when given the opportunity to predict a specific word, participants in the present study displayed a rather right-lateralized distribution of cortical brain activity. Notably, this right-lateralization of a predictive effect is in line with two consecutive EEG studies by Otten and colleagues (Otten, Nieuwland, & Van Berkum, 2007; Otten & Van Berkum, 2009). Otten et al. investigated the electrophysiological responses of participants exposed to context that strongly suggested the appearance of a specific target noun (e.g. Otten & Van Berkum, 2009, original in Dutch: "The actress wore a beautiful dress, but she thought her neck was a little plain. She picked up **the**$_{\text{gender-marked}}$ delicate yet striking **necklace** that had been selected by her stylist."; target determiner and noun in bold-face) and either presented the predictable adjective/determiner and target word or an unpredicted target noun with a different gender (and a differently gender-marked adjective/determiner). The authors reported mismatch responses already at the wrong-inflected adjectives/determiners preceding the predictable target noun – and this mismatch positivity was distributed across the right frontal hemisphere. Of course the distribution of an ERP response does not directly allow inferring the location of its underlying neural generator; however the present study provides new evidence that the right hemisphere takes part in generating linguistic predictions online. So far, the right hemisphere has been linked to various aspects of linguistic processing, such as dealing with prosody and paralinguistic information as well as visual word recognition (for a comprehensive review, see Lindell, 2006). Further research would be needed to investigate whether or not the right hemisphere might subserve a special, prediction-related role in sentence comprehension.

In summary, the integrative framework for language comprehension and production is a comprehensive theoretical approach that highlights the interdependence of comprehension and production processes and explicitly implies a predictive component. Most of the neurophysiological findings from the present fMRI prediction study are in line with Pickerings and Garrods theory, but extending it by suggesting a role of sequence processing systems and the language-related regions of the right hemisphere in generating linguistic predictions.

5.2.2 CRITICAL REFLECTIONS

The most apparent critique regarding the syntactic prediction study described in chapter 4 is the absence of a semantic prediction condition. The study contained one condition containing semantic and syntactic cues, one condition containing only syntactic cues, and one condition without any cues for linguistic predictions – thus, for a full two-by-two design crossing syntax and semantics, a fourth condition containing purely semantic predictions is missing. To fill this gap, a second experiment investigating semantic predictions was conducted during the last part of the present PhD thesis (see Methods section 2.4.3). In this experiment, instead of judging the grammaticality of the target word, the participants' task was to decide whether or not the target word was a valid continuation of the preceding word sequence with regard to two semantic categories (i.e., winter or summer). Again, winter and summer target words (such as 'Sauna/*sauna*' versus 'Sonne/*sun*') were presented at distinct locations on the screen. Predictive processes under three conditions were compared: sentences, purely semantics, and non-word lists. The purely semantic condition was (similar to the meaningless jabberwocky condition used in the syntactic prediction study) created based on the normal sentences by retaining all content words (in their basic form) and exchanging all function words.

Interestingly, in this experiment, the predictive eye gazes during the delay were equally fast in the sentence condition and in a 'pure semantic' condition. On a first glance, this suggests that in the condition with less linguistic cues (i.e., semantic cues only), the predictive process was equally as fast as in the condition that provided both syntactic and semantic cues, which seems to contradict the results from the experiment investigating syntactic predictions: Adding linguistic cues was expected to improve linguistic prediction. However, there is a fundamental difference between the two studies regarding the time point of the semantic vs. syntactic prediction. In principle, in both sentences and purely semantic items the prediction regarding the semantic category of the target word can be made at the first cue word with semantic associations regarding winter or summer. This cue word was placed at various positions within the word sequence to assure sustained attention of the participants during word sequence processing; however, this implicates that the semantic prediction is not necessarily generated during the delay phase. As the eye gaze reading paradigm aimed at disentangling the predictive process from ongoing perceptual processing, the predictive process ideally should be triggered right before the delay. Thus, the first indicator for the semantic category would necessarily have to be the last word of the word sequence. However, as participants would have noticed soon that they only needed to attend to the last word preceding the target word in the semantic condition, assuring equal attention/processing levels across conditions would be impossible. Thus, the first semantic cue word necessarily needed to be at different positions within the word sequence. For future studies, it should be tested whether or not including a low percentage of catch trials with cue words at earlier positions is sufficient to prevent the before mentioned effect.

To sum up the major limitations of the prediction study described in chapter 4, on the one hand, the study missed a condition tackling purely semantic predictions. On the other hand, transferring the paradigm to the semantic prediction domain raised one important issue: Although the existence of semantic predictions can be evidenced by anticipatory eye movements during the delay period before target word presentation, the actual semantic prediction was possible already earlier in the word sequence. In consequence, the eye movements during the delay in the present semantic prediction study (section 2.4.3) probably do not reflect the timing of the actual prediction process and thus cannot be used as timing information for the fMRI model. In general, it might be questioned whether or not aligning the timing of the prediction phase in the fMRI model to the anticipatory eye movements actually captures the predictive process. The following list provides four arguments, why this approach is considered a valid approximation of actual timing of the predictive process for the fMRI model in the present syntactic prediction study:

1. Without the information provided by anticipatory eye movements, no indication regarding the timing of the predictive process is available for analysis.
2. Compared to the time-sensitivity of EEG, the exact timing of each trial is less important in fMRI, because the BOLD response measured in fMRI is relatively sluggish. For example, even if the actual predictive process would start on average 200ms earlier than the eye movement or if the onset of the eye movement was not perfectly aligned to

the onset of the predictive process in every trial, the effect should be captured with fMRI nevertheless.

3. Aligning the timing of the prediction phase to the actual eye movement in each trial assures that in all conditions (sentences, jabberwocky, and non-word lists) participants move their eyes. When the conditions are directly contrasted to (i.e., subtracted from) each other, all neurophysiological activity going back to simple eye movements cancels out.
4. As described in chapter 4.4, consecutive phases of trials are inherently correlated with respect to their timing (i.e., the prediction phase always follows the word sequence presentation, and this order is never reversed). Thus the analysis of consecutive phases suffers from severe multicollinearity issues (cf. Schon et al., 2009), if the trial phases are not jittered in time. In order to find BOLD activation belonging to a specific trial phase, an inter-phase jitter has to be included in the fMRI model. Aligning the onset of the prediction to the eye movement in the respective trial phase automatically introduces a time jitter between word string presentation and prediction phase, which naturally varies across trials and thus solves the multicollinearity issue outlined above.

The present chapter so far summarized and discussed the results of the working memory and the sentence study separately; however, as argued in the introduction, generating a prediction is highly dependent on the availability of knowledge stored in memory and activated by current input. Therefore, the following section aims at linking the memory and prediction processes observed in the current studies.

5.3 PREDICTION AND MEMORY: DEPENDENCIES AND SHARED NEURAL RESOURCES

Already in the early 1990ies, in their theoretical framework of long-term working memory (LT-WM), Ericsson and Kintsch pointed at the benefits that selecting and keeping up important information from previous input might have for processing upcoming information. Investigating highly skilled individuals which expanded their working memory capacities in specific areas (e.g. remembering positions on a checker board or very long number sequences), the authors claim certain priors for such an extended working memory:

"…subjects must be able to rapidly store information in LTM [long term memory]*; this requires a large body of relevant knowledge and patterns for the particular type of information involved." (Ericsson & Kintsch, 1995, p. 215)*

Given the massive amount of practice over decades, it is safe to assume that human adults can all be considered experts when it comes to their native language. Ericsson and Kintsch continue with suggesting a second precondition for superior memory skills:

"… the activity must be very familiar to the experts because only then can they accurately anticipate future demands for retrieval of relevant information ." (Ericsson & Kintsch, 1995, p. 215)

Basically, Ericsson and Kintsch proposed that memory experts use their long term memory to store large amounts of information – and that anticipating future demands might be helpful to ease future memory access. In a more recent work, Moshe Bar (Bar, 2007, 2009) inverses this argument by suggesting that one of the purposes (or main advantages) of remembering information is that memory enables us to anticipate future situations. The author argues that predictions are generated based on analogies to earlier experienced events. In line with this proposal, Schacter and colleagues propose that the ability to simulate or imagine future events is based on episodic memory (Schacter et al., 2007; Schacter et al., 2012). Transferring this logic into the domain of language, human adults do not only possess a large set of cognitive models of the world and rich semantic background knowledge, they are also well-experienced in perceiving and producing their native language. In sum, human adults are well-equipped to generate predictions about future language input. These predictions might even be alleviated by the fact that in language, information is provided in a syntactically structured way: The studies presented in chapters 3 and 4 demonstrate that sentence structure allows for easier chunking of previous information and also anticipating missing upcoming input.

Although a growing body of research focuses on either predictive processing or memory, there have been only few studies attempting to directly link prediction and memory in the linguistic domain. Studies by Linderholm (2002) and Estevez and Calvo (2000) were able to show that individuals with high working memory capacity generated predictive inferences faster and more reliably than low-span individuals.

However, those studies focused on a different type prediction, so-called predictive inferences (implicit, causal implications of a text, e.g. "While shooting a film, the actress accidentally fell out of the 14th floor window" leading to the predictive inference that the actress died in consequence; see van den Broek, 1990, 1994). The only study investigating the dependency of generating word predictions during discourse reading on the individual working memory capacity so far is an EEG study by Otten and van Berkum (2009). The authors presented their subjects with mini-scenarios consisting of two sentences. The first sentences provided a highly predictive context for the appearance of a specific target noun in the second sentence. Notably, when time-locking the ERP analysis to the determiner preceding the noun target in the second sentence, a violation of the gender agreement between the actually presented determiner and the predicted noun already led to a difference in brain responses. This result suggests that readers indeed generate online expectations about upcoming words. Additionally, the responses differed for low and high WMC individuals – whereas both groups demonstrated an early mismatch response, only the low WMC group showed a later positive deflection. Thus, the initial response of both groups is similar (i.e., all subject generate a prediction and detect a respective violation), but the subsequent processing of information differs between high- and low-span individuals.

In contrast to Otten & Van Berkum (2009), the present experiments were designed to identify the neural resources underlying the memory and prediction processes. Although EEG measurements are an excellent choice for investigating the time course of fast brain processes, the method is not equally well suited to identify the brain areas supporting these processes. Thus the following section will add some new evidence for a potential shared network of memory and prediction by comparing the neuronal activation pattern found in the present working memory and prediction study.

5.3.1 SHARED NEURAL RESOURCES FOR WORKING MEMORY AND PREDICTION

The two studies reported in the present thesis investigated memory and prediction in sentence processing separately; however, as argued in the previous section, prediction is inherently linked to memory. For this reason, it has been hypothesized that both processes partly draw on the same neural resources: For example, Randy Buckner (Buckner, 2010) proposed that the hippocampal system might not only support memory processes, but also might be a fruitful candidate for playing a role in generating predictions. The present section thus will provide a short supplementary analysis singling out the shared neural resources playing a role in both the deeper encoding of syntactically structured word sequences (i.e., part-sentences as compared to ungrammatical word sequences; cf. chapter 3) as well as the prediction of missing grammatical elements (in a sentence or jabberwocky context; cf. chapter 4).

Methods. In order to investigate whether sentence structure triggers engagement of the same neural resources in both encoding of sentences and prediction of syntactic elements in a sentence context, fMRI data from the prediction phase of the syntactic prediction experiment was analyzed together with fMRI data from the encoding phase of the working memory experiments.

Specifically, the activation clusters found in the prediction study (i.e., results from a conjunction analysis examining the brain regions underlying syntactic predictions in normal and jabberwocky contexts, cf. chapter 4.5.3) were inclusively masked with the activation clusters from the encoding phase of the working memory study (i.e. those brain regions showing stronger activation for sentence than ungrammatical word sequences). All other methodological parameters, such as for example fMRI scanning parameters, subject pool, fMRI preprocessing and fMRI model are identical to the studies described in chapter 3-4, thus for a more detailed description the interested reader is referred to the respective methods and results sections in the manuscripts (sections 3.3 - 3.4 and 4.3 - 4.5). In summary, the additional masked contrast calculated for the present section reveals all shared brain resources used during the encoding of words in a sentence structure and the prediction of missing syntactic elements in sentences.

Results and interpretation. As illustrated in Figure 5.1 and Table 5.1, a subset of brain areas used in the prediction of missing syntactic elements are also involved in encoding a syntactically structured sequence (in the present case, a half-sentence). Specifically, part of the left angular gyrus, left putamen, bilateral hippocampi (extending into amygdalae) and the right cerebellum are involved in encoding and prediction. The following paragraph will integrate these results with existing hypotheses regarding the functions of the mentioned areas in memory and prediction.

The left angular gyrus is regarded necessary for reading (e.g. Horwitz, Rumsey, & Donohue, 1998) and sentence comprehension (Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004); it has been subscribed a role in lexical access (Binder et al., 2003) and in semantic processing (Binder et al., 2009) and syntax comprehension (e.g., thematic role checking, Newhart et al., 2012; or processing syntactic ambiguities, Tyler et al., 2011). Binder and colleagues summarize the functions of the angular gyrus under the label “complex information integration and knowledge retrieval" (Binder et al., 2009; p. 2776). In line with the latter proposal, the angular gyrus has also been observed to support working memory processes (Ranganath, Johnson, & D'Esposito, 2003). Taken together, the angular gyrus seems to be well-suited to support linguistic memory and integration processes; additionally, its activation level has also been shown to vary with semantic predictability (Obleser, Wise, Dresner, & Scott, 2007), and it is part of the hippocampal prediction network proposed by Buckner (Buckner, 2010).

Indeed, as discussed above, many neurophysiological concepts of memory, prediction, simulation and imagination suggest a vital role of the hippocampus in these processes (e.g. Buckner, 2010; Mullally & Maguire, 2014; Schacter et al., 2007; Schacter et al., 2012). The cerebellum has been linked to predictive processes in past years as well; however, although most of the research focuses on predictions in the motor domain (Bastian, 2006), there is some evidence that the cerebellum helps to optimize/recalibrate predictions about upcoming sensory events in a non-motor task (Roth, Synofzik, & Lindner, 2013). Additionally, the cere-

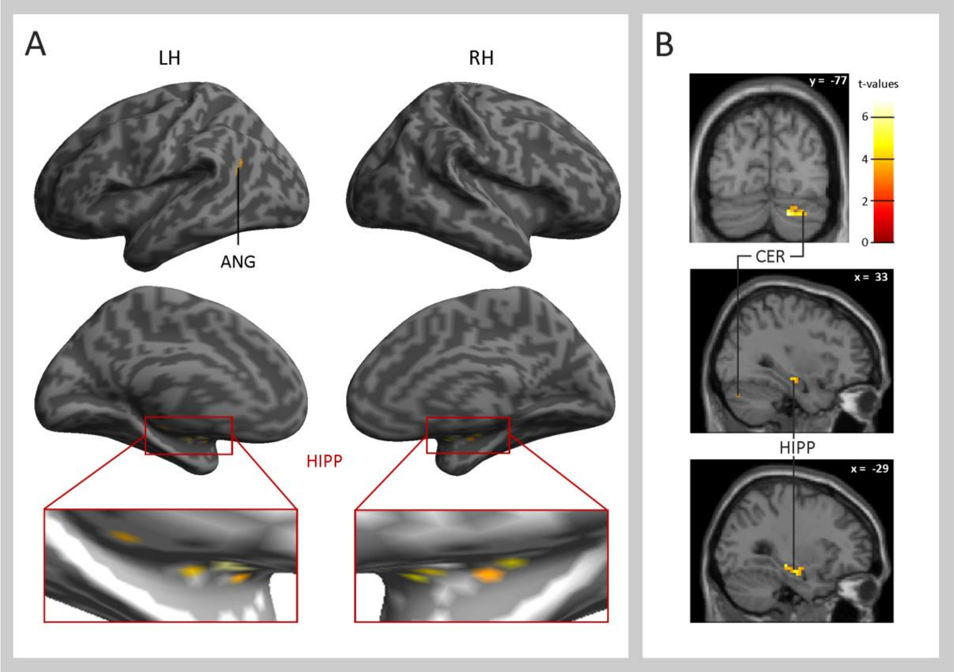

Figure 5-1: fMRI activation pattern. Conjunction analysis of neurophysiological activation indicating the brain regions supporting word category prediction (i.e, sentences > non-word lists & jabberwocky > non-word lists), masked exclusively with areas that were activated stronger during the encoding of sentences as compared to the encoding of ungrammatical strings. Panel A: Rendered images showing cortical activity; Panel B: Slices illustrating HIPP and CER activation. ANG, angular gyrus; CER, cerebellum; HIPP, hippocampus; LH, left hemisphere; RH, right hemisphere.

bellum has been assigned a vital role in other cognitive processes, among them different aspects of language processing (such as e.g. reading, word-finding, and naming; see De Smet, Paquier, Verhoeven, & Marien, 2013). In addition, based on the present data, the cerebellum seems to be involved in encoding sentences and predicting missing syntactic items.

In summary, the present results suggest that encoding words in a syntactic structure and predicting upcoming syntactic elements partly rely on shared neural resources. Specifically, the hippocampus, angular gyrus, and the cerebellum play a role in both aspects of sentence structure processing.

Table 5-1: Activation clusters and peak voxels for the masked conjunction analysis.

Brain region	Hemisphere	Cluster size (voxel)	BA	z_{max}	MNI coordinates		
					x	y	z
Angular gyrus	L	13	39	4.03	-42	-58	22
Putamen	L	14	-	3.90	-33	-7	-5
Basal ganglia/medial temporal lobe	R	40					
Amygdala	R		-	5.64	27	-4	-11
Hippocampus	R		-	4.29	33	-16	-14
Basal ganglia/medial temporal lobe	L	30					
Amygdala	L		-	4.77	-24	-4	-14
Hippocampus	L		-	4.79	-30	-25	-11
Cerebellum	R	32	-	6.44	15	-79	-32

Limitations. Although the results are in line with previous work on prediction and memory, there is a serious limitation to the analysis described above: not only the condition (prediction vs. encoding) varied between the two studies, but also the participant pool, and even more importantly, the item set. For this reason, more sophisticated analyses functionally linking the activity in the reported areas are not advised in the present data set. However, on the other hand, the fact that the present analysis was successful in identifying common brain regions for predictive and memory processes across participant groups and item sets might be taken as a motivation to conduct further studies varying both aspects in one experiment in the future: The present results might underestimate the actual effect (and the network involved) due the disturbance variance introduced by different subject groups and item sets.

5.4 CONCLUSION AND OUTLOOK

Successful communication requires the ability to remember and maintain previous contents while processing language processing online. Additionally, recent concepts of brain functioning suggest that the brain utilizes current input and pre-existing knowledge to simultaneously anticipate upcoming perceptions, relying on internal models of the world generated from prior analogous experiences. Both memorizing sentences and predicting upcoming linguistic information were investigated in the present thesis. Memorizing sentences was examined on the basis of the sentence superiority effect (i.e. the observation that within sentences, humans are able to recall a significantly larger number of words than in word lists). Results from a working memory task and simultaneously acquired fMRI data are in line with the theoretical proposal that sentences automatically trigger an enriched memorizing process in which the sentence structure presumably is used to bind the single words into larger, meaningful chunks by the means of semantic brain network and the hippocampal/parahippocampal formation. This enriched encoding process lowers the working memory load and the demands on cognitive control and attention during maintenance of sentences (as compared to word lists). This interpretation of the two-fold pattern of neurophysiological engagement was supported by behavioral results: The high performance in sentences combined with the observation that sentence structure lowers/eliminates the detrimental effects of additional working memory load and the prevention of rehearsal strategies speak to the power of syntactic structure for working memory.

To investigate the second major topic of the present thesis, that is predictive processes during sentence processing, a new predictive eye gaze reading task was introduced, which allows to examine linguistic predictions separately from ongoing perceptual linguistic processing. The new neurophysiological and eye tracking evidence obtained based on the predictive eye gaze reading task was in line with the predictive coding framework: Brain regions commonly reported for language and sequence processing were also engaged in generating predictions regarding future linguistic input. In general, the findings are consistent with a number of other recent studies that suggest a potential role of linguistic predictions in language processing: Especially the speed of linguistic processing might be understood in terms of predictive processing (cf. Pickering & Garrod, 2013).

Although the present studies investigated memory for and prediction in sentences separately, those processes might not be as independent after all. The predictive coding framework relies on the assumption that predictions are generated based on internal models, which are stored in our memory; thus current perceptual input might trigger activation of memory contents which in turn co-activate highly probable co-existing or following percepts – a predictive process. The present results support this assumption in showing that the hippocampus is involved in encoding syntactically structured material in a working memory task, but also when upcoming elements of a syntactically structured sequence are predicted. Randy Buckner (2010) suggested that the neurophysiological system underlying memory actually provides the basis for constructing a prediction: a hippocampal-cortical system, involving areas such as parahippocampus, entorhinal cortex, middle temporal cortex, inferior parietal areas. Notably, the regions considered part of the hippocampal-cortical system coincide largely with those regions activated during encoding of sentences and predicting missing syntactic elements during the present study: Not only the hippocampus, but also inferior parietal lobe and the cerebellum were involved in both experimental conditions.

However, there was a remarkable difference in cortical activity between encoding and predicting linguistic material in the present studies regarding their predominant lateralization: In contrast to encoding sentences, predicting words led to more pronounced and widespread activity of the cortical language processing areas in the right hemisphere than in their left-hemispheric homologues. Overall, the present studies might stimulate further research in the following areas:

1. The role of left- and right-hemispheric language regions: Are right-hemispheric contributions essential to predictive linguistic processes?
2. The contributions of top-down predictive and bottom-up linguistic processes during sentence comprehension should be investigated more closely, as it remains an open question, which parts of the neurophysiological activation typically seen in sentence comprehension studies go back to which type of processing.
3. In the present studies, Broca's area neither showed specific engagement during sentence encoding (compared to ungrammatical word sequence encoding) into working memory, nor did it differentially support the prediction of specific words in a sentence (as compared to the prediction of syntactic elements or no prediction whatsoever). However, when a prediction of an upcoming syntactic category was generated based on syntactic cues only (i.e., in the context of jabberwocky), Broca's area was engaged; and it has also been repeatedly reported for processing of complex syntactic structures, where one might speculate that automatic prediction of upcoming words often fails. Thus, it would be interesting to further investigate whether Broca's area actually takes action in a compensatory manner if syntax is the only or the most important/overriding factor for sentence comprehension.

4. In order to specify the role of prediction in language comprehension and production, a potential next step could involve finding a way to experimentally investigate the combined constraints of various linguistic features (such as e.g. syntax, semantics, or phonology) on prediction that benefit processing speed and capacity. From a predictive-processing perspective, processing numerous types of linguistic information (instead of focusing solely on e.g. semantics) is economic, because the more constraints from different areas are available, the more precise the prediction, and the less effortful the future processing. However, investigating predictions based on combinations of cues is experimentally challenging. For example, when investigating predictions based on combined semantic and syntactic constraints, one has to deal with the possibility that they operate on different time scales and different extents of information: while a purely syntactic prediction might be rather local, a semantic prediction might span across many sentences, generated based on the whole preceding discourse. In a context providing both syntactic and semantic cues one might speculate that the rather abstract prediction of potential meaningful content is specified via syntactic information thereby rendering its current perceptual form predictable (e.g. "Hund – spielen – Kind – grün → Wiese?" vs. "Der Hund spielte mit dem Kind auf der grünen → Wiese?").
5. Whether or not working memory and prediction processes for sentences rely on the same neural resources should be investigated in more detail in a separate study that allows varying both processes within the same item set and participant pool. This approach would render more sophisticated analyses possible, such as for example functional connectivity analyses between the areas involved in both types of processes.
6. Finally, expanding the scope of the present thesis, future research might focus on the question whether or not the ability to predict upcoming words is a key factor to excellent language skills. Following this line of argumentation, increasing language skills of children during acquisition of their native language (potentially, but not necessarily extending to adolescents or adults acquiring their second or third language) should be accompanied by more extensive, accurate and automatized predictive processing.

In conclusion, the present results expand the understanding of simultaneous processes during language comprehension by describing the processes underlying the memorization of previous information as well as the anticipation of future linguistic input; moreover, they provide first evidence for shared neural resources supporting both types of processes.

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ABBREVATIONS

ACC	anterior cingulate cortex	PCS	precentral sulcus
ANG	angular gyrus	PFC	prefrontal cortex
AS+	condition with Articulatory Suppression	PI	Purkinje image
AS -	condition without Articulatory Suppression	PRED	prediction phase
CIM	causal inference maker	PUT	putamen
CRH	conceptual regeneration hypothesis	RH	right hemisphere
fMRI	functional magnetic resonance imaging	RT	response time
GLM	general linear model	SEM	semantic condition (without function words)
HIPP	hippocampus	SENT	normal sentences
hiWML	high working memory load	SMA	supplementary motor area
INS	insula	SSE	sentence superiority effect
IPS	intra-parietal sulcus	SST+	half-sentences
JAB	jabberwocky sentences	SST-	ungrammatical word sequences
LH	left hemisphere	STM	short-term memory
loWML	low working memory load	TASK	task phase of the prediction study
LTM	long-term memory	THAL	thalamus
LT-WM	long-term working memory	TR	repetition time
MNI	Montreal Neurological Institute	TWA	target word area
MR	magnetic resonance	WM	working memory
MTG	middle temporal gyrus	WML	working memory load
NWL	non-word lists	WSP	word sequence presentation

6 APPENDIX

6.1 STIMULUS SETS

6.1.1 PROJECT 1: REMEMBERING SENTENCES VERSUS WORD STRINGS

Table 6-1: Stimulus set for project 1 (investigating the sentence superiority effect in working memory tasks). 1-6, words or sign strings; Item quartet, high- and low working memory load version of an item in a grammatical or ungrammatical word order; SST, sentence structure (+, grammatical; -, ungrammatical); WML, working memory load.

Item quartet	WML	SST	1	2	3	4	5	6
1	low	+	+-+-+	-+-+-	er	ist	ihm	gestern
	low	-	+-+-+	-+-+-	er	gestern	ihm	ist
	high	+	er	ist	ihm	gestern	Morgen	beim
	high	-	er	beim	Morgen	gestern	ihm	ist
2	low	+	+-+-+	-+-+-	sie	hat	ihn	zum
	low	-	+-+-+	-+-+-	sie	zum	ihn	hat
	high	+	sie	hat	ihn	heute	Abend	zum
	high	-	sie	zum	Abend	heute	ihn	hat
3	low	+	+-+-+	-+-+-	sie	sollen	ihr	bei
	low	-	+-+-+	-+-+-	sie	bei	ihr	sollen
	high	+	sie	sollen	ihr	morgen	Abend	bei
	high	-	sie	bei	Abend	morgen	ihr	sollen
4	low	+	+-+-+	-+-+-	sie	darf	ihnen	morgen
	low	-	+-+-+	-+-+-	sie	morgen	darf	ihnen
	high	+	sie	darf	ihnen	nur	morgen	Mittag
	high	-	sie	Mittag	morgen	nur	ihnen	darf
5	low	+	+-+-+	-+-+-	er	würde	morgen	am
	low	-	+-+-+	-+-+-	er	am	würde	morgen
	high	+	er	würde	doch	morgen	am	Abend
	high	-	er	Abend	am	morgen	doch	würde
6	low	+	+-+-+	-+-+-	er	soll	sie	heute
	low	-	+-+-+	-+-+-	er	heute	sie	soll
	high	+	er	soll	sie	doch	heute	Morgen
	high	-	er	Morgen	heute	doch	sie	soll
7	low	+	+-+-+	-+-+-	es	wurde	gestern	am
	low	-	+-+-+	-+-+-	es	am	gestern	wurde
	high	+	es	wurde	dann	gestern	Abend	bei
	high	-	es	bei	Abend	gestern	dann	wurde
8	low	+	+-+-+	-+-+-	sie	wurden	gestern	bei
	low	-	+-+-+	-+-+-	sie	bei	gestern	wurden
	high	+	sie	wurden	gestern	Abend	an	der

Item quartet	WML	SST	1	2	3	4	5	6
	high	-	sie	der	an	Abend	gestern	wurden
9	low	+	+-+-+	-+-+-	heute	hat	er	bei
	low	-	+-+-+	-+-+-	heute	bei	hat	er
	high	+	heute	hat	er	es	bei	der
	high	-	heute	der	bei	es	er	hat
10	low	+	+-+-+	-+-+-	heute	soll	er	es
	low	-	+-+-+	-+-+-	heute	es	er	soll
	high	+	heute	Morgen	soll	er	es	zur
	high	-	heute	zu	es	er	soll	Morgen
11	low	+	+-+-+	-+-+-	heute	wurde	sie	an
	low	-	+-+-+	-+-+-	heute	an	sie	wurde
	high	+	heute	Morgen	wurde	sie	an	der
	high	-	heute	der	an	sie	wurde	Morgen
12	low	+	+-+-+	-+-+-	heute	kann	er	es
	low	-	+-+-+	-+-+-	heute	es	er	kann
	high	+	heute	Abend	kann	er	es	an
	high	-	heute	an	es	er	kann	Abend
13	low	+	+-+-+	-+-+-	morgen	werden	sie	ihm
	low	-	+-+-+	-+-+-	morgen	ihm	sie	werden
	high	+	denn	morgen	Abend	werden	sie	ihm
	high	-	denn	ihm	sie	werden	Abend	morgen
14	low	+	+-+-+	-+-+-	morgen	würde	sie	ihn
	low	-	+-+-+	-+-+-	morgen	ihn	sie	würde
	high	+	erst	morgen	Mittag	würde	sie	ihn
	high	-	erst	ihn	sie	würde	Mittag	morgen
15	low	+	+-+-+	-+-+-	morgen	darf	er	sie
	low	-	+-+-+	-+-+-	morgen	sie	er	darf
	high	+	dann	darf	er	sie	morgen	Mittag
	high	-	dann	Mittag	morgen	es	er	darf
16	low	+	+-+-+	-+-+-	gestern	ist	sie	ihm
	low	-	+-+-+	-+-+-	gestern	ihm	sie	ist
	high	+	gestern	Morgen	ist	sie	bei	ihm
	high	-	gestern	ihm	bei	sie	ist	Morgen
17	low	+	+-+-+	-+-+-	gestern	durfte	er	es
	low	-	+-+-+	-+-+-	gestern	es	er	durfte
	high	+	gestern	Morgen	durfte	er	es	dann
	high	-	gestern	dann	es	er	durfte	Morgen
18	low	+	+-+-+	-+-+-	wollen	sie	ihr	morgen
	low	-	+-+-+	-+-+-	wollen	morgen	ihr	sie
	high	+	wollen	sie	ihr	morgen	Abend	beim
	high	-	wollen	beim	Abend	morgen	ihr	sie
19	low	+	+-+-+	-+-+-	musste	er	sie	zur
	low	-	+-+-+	-+-+-	musste	zur	sie	er
	high	+	musste	er	sie	gestern	Abend	zur
	high	-	musste	zur	Abend	gestern	sie	er

Item quartet	WML	SST	1	2	3	4	5	6
20	low	+	+-+-+	-+-+-	kann	er	es	morgen
	low	-	+-+-+	-+-+-	kann	morgen	es	er
	high	+	kann	er	es	morgen	Abend	noch
	high	-	kann	noch	Abend	morgen	es	er
21	low	+	+-+-+	-+-+-	darf	sie	ihn	heute
	low	-	+-+-+	-+-+-	darf	heute	ihn	sie
	high	+	darf	sie	ihn	dann	heute	Morgen
	high	-	darf	Morgen	heute	dann	ihn	sie
22	low	+	+-+-+	-+-+-	will	er	ihn	von
	low	-	+-+-+	-+-+-	will	von	ihn	er
	high	+	will	er	ihn	morgen	Abend	von
	high	-	will	von	Abend	morgen	ihn	er
23	low	+	+-+-+	-+-+-	soll	es	ihr	heute
	low	-	+-+-+	-+-+-	soll	heute	es	ihr
	high	+	erst	heute	Abend	soll	es	ihr
	high	-	erst	ihr	es	soll	Abend	heute
24	low	+	+-+-+	-+-+-	wollte	sie	ihm	gestern
	low	-	+-+-+	-+-+-	wollte	gestern	ihm	sie
	high	+	wollte	sie	ihm	erst	gestern	Abend
	high	-	wollte	Abend	gestern	erst	ihm	sie
25	low	+	+-+-+	-+-+-	wen	durften	sie	von
	low	-	+-+-+	-+-+-	wen	von	sie	durften
	high	+	wen	durften	sie	gestern	Morgen	von
	high	-	wen	noch	Morgen	gestern	sie	durften
26	low	+	+-+-+	-+-+-	was	würde	ihnen	heute
	low	-	+-+-+	-+-+-	was	heute	ihnen	würde
	high	+	was	würde	ihnen	denn	heute	Mittag
	high	-	was	Mittag	heute	denn	ihnen	würde
27	low	+	+-+-+	-+-+-	wo	wurde	sie	gestern
	low	-	+-+-+	-+-+-	wo	gestern	sie	wurde
	high	+	wo	wurde	sie	gestern	Abend	von
	high	-	wo	von	Abend	gestern	sie	wurde
28	low	+	+-+-+	-+-+-	wen	müssen	sie	denn
	low	-	+-+-+	-+-+-	wen	denn	sie	müssen
	high	+	wen	müssen	sie	denn	morgen	Abend
	high	-	wen	Abend	morgen	denn	sie	müssen
29	low	+	+-+-+	-+-+-	wem	kann	sie	morgen
	low	-	+-+-+	-+-+-	wem	morgen	kann	sie
	high	+	zu	wem	kann	sie	morgen	Abend
	high	-	zu	Abend	morgen	sie	kann	wem
30	low	+	+-+-+	-+-+-	wo	sollte	sie	ihr
	low	-	+-+-+	-+-+-	wo	ihr	sie	sollte
	high	+	wo	sollte	sie	ihr	gestern	Abend
	high	-	wo	Abend	gestern	ihr	sie	sollte

6.1.2 PROJECT 2: PREDICTING WORDS AND SYNTACTIC CATEGORIES

Table 6-2: Stimulus set for project 2 (investigating word and syntactic word category prediction). JAB, meaningless jabberwocky sentences; NWL, non-word lists; SENT, normal sentences; Item set, participants were exposed to either item set A or B.

Item sextett	Normal sentences (SENT), jabberwocky sentences (JAB), and non-word lists (NWL)	Target word	Condition	Syllable count	Item set
1	Das Model bevorzugte gesund statt fettig zu	**essen**/Essen	SENT	13	A
1	Das Model mochte stets gesundes statt fettiges	essen/**Essen**	SENT	13	B
1	Das Mostitt bevorzugte sundge fe delttig zu	**essen**/Essen	JAB	13	B
1	Das Stitsmoch stitte mo delgedes fe sunttiges	essen/**Essen**	JAB	13	A
1	Be mostitt Tezuzagdas sundge fe delvor tig	**essen**/Essen	NWL	13	B
1	Te stitsmoch Stittges mo delgedas fe sundesti	essen/**Essen**	NWL	13	A
2	Seit Geburt konnte der Prinz immer sorgenfrei	**leben**/Leben	SENT	12	A
2	Seit Geburt hatte der Prinz ein sorgenfreies	leben/**Leben**	SENT	12	B
2	Seit Merfrie konnte der Sor genim burtgepronz	**leben**/Leben	JAB	12	B
2	Seit Hafrie gente der Sor ein burtgepronzes	leben/**Leben**	JAB	12	A
2	Te merfrie Derseut Konn sor genim burtgepronz	**leben**/Leben	NWL	12	B
2	Te hafrie Genein Ge sorr burt deresseutpronz	leben/**Leben**	NWL	12	A
3	Er konnte die Taubheit in den Fingerspitzen	**fühlen**/Gefühl	SENT	12	A
3	In den Fingerspitzen hatte er ein taubes	fühlen/**Gefühl**	SENT	12	B
3	In den Hafongtautzen ertte er ein spibes	**fühlen**/Gefühl	JAB	12	B
3	Er konnte die Fongheit in den Spitaubertzen	fühlen/**Gefühl**	JAB	12	A
3	Te Denin konn ertzen Fong heit spitauberdie	**fühlen**/Gefühl	NWL	12	B
3	Bes ha ereinteden dentzen fong Spi intau	fühlen/**Gefühl**	NWL	12	A
4	Nach dem Abitur plante sie Medizin zu	**studieren**/Studium	SENT	12	A
4	Nach dem Abitur wählte sie Medizin als	studieren/**Studium**	SENT	12	B
4	Nach dem Dimebi plante sie Zintura zu	**studieren**/Studium	JAB	12	B
4	Nach dem Dimewöhl bite sie Zintura als	studieren/**Studium**	JAB	12	A
4	Plin Te dimenach demsie zin Zutura bi	**studieren**/Studium	NWL	12	B
4	Wöhl Te dimenach demsie zin Alstura bi	studieren/**Studium**	NWL	12	A

Item sex-tett	Normal sentences (SENT), jabberwocky sentences (JAB), and non-word lists (NWL)	Target word	Condition	Syllable count	Item set
5	Durstig begann der abstinente Säufer Wasser zu	**trinken**/Getränk	SENT	14	A
5	Durstig wählte der abstinente Säufer Wasser als	trinken/**Getränk**	SENT	14	B
5	Säutig begann der wastisserte Dursab Nenfer zu	**trinken**/Getränk	JAB	14	B
5	Säutig wate der wöhlstisserte Dursab Nenfer als	trinken/**Getränk**	JAB	14	A
5	Säuder Zube te Wastissergann dursab nenfer tig	**trinken**/Getränk	NWL	14	B
5	Säute Alswa te Wöhlstisserder dursab nenfer tig	trinken/**Getränk**	NWL	14	A
6	Bei Windaufkommen konnte man mit ihrem Boot	**segeln**/Segel	SENT	12	A
6	Im Boot benutzte man bei Windaufkommen das	segeln/**Segel**	SENT	12	B
6	Bei Fooraufwondmen konnte man mit ihrem Kom	**segeln**/Segel	JAB	12	B
6	Im Kom wondaufte man bei Foornatzbemen das	segeln/**Segel**	JAB	12	A
6	Konn Fooraufwondman Beirem te men mitih kom	**segeln**/Segel	NWL	12	B
6	Te Kom Bufimman foor Wond menbeibedas natz	segeln/**Segel**	NWL	12	A
7	Sie wollte das Auto nicht am Straßenrand	**parken**/Parkplatz	SENT	11	B
7	Am Straßenrand gab es für Autos einen	parken/**Parkplatz**	SENT	11	A
7	Am Rondaustra sen es für Tosgab einen	**parken**/Parkplatz	JAB	11	A
7	Sie wollte das Toßen nicht am Rondaustra	parken/**Parkplatz**	JAB	11	B
7	Te Amdas au toßen Rond wull sienuchtstra	**parken**/Parkplatz	NWL	11	A
7	Stra Nenfürei Sen rond tos augab esam	parken/**Parkplatz**	NWL	11	B
8	Ohne Brot mussten in Afrika viele Kinder	**hungern**/Hunger	SENT	13	B
8	In Afrika verringerte Brot bei Kindern den	hungern/**Hunger**	SENT	13	A
8	Ohne Kin mussten in Kabreta viele Frider	**hungern**/Hunger	JAB	13	A
8	In Rinbreta kafriverte Kin bei Gerdern den	hungern/**Hunger**	JAB	13	B
8	Tenvie Kin Derle Ne kabreta mussin frider	**hungern**/Hunger	NWL	13	A
8	Te Rinbreta Kafriderin kin Ver gerbei dern	hungern/**Hunger**	NWL	13	B
9	Der Pilot konnte auch einen großen Airbus	**fliegen**/Flugzeug	SENT	12	A
9	Der Pilot des Airbus begrüßte alle im	fliegen/**Flugzeug**	SENT	12	B
9	Der Lotgro konnte auch einen ärßen Buspi	**fliegen**/Flugzeug	JAB	12	B
9	Der Lotgräß des Buspi ärbete alle im	fliegen/**Flugzeug**	JAB	12	A
9	Konn Lotgro Derßen te nenauch ärei buspi	**fliegen**/Flugzeug	NWL	12	B

Item sextett	Normal sentences (SENT), jabberwocky sentences (JAB), and non-word lists (NWL)	Target word	Condition	Syllable count	Item set
9	Lot dergräß Bus allepi Ärdesim te be	fliegen/**Flugzeug**	NWL	12	A
10	Unter dunklen Wolken begann es heftig zu	**regnen**/Regen	SENT	12	A
10	Am Tag brachten dunkle Wolken den heftigen	regnen/**Regen**	SENT	12	B
10	Unter heflen Duncken begann es woltig zu	**regnen**/Regen	JAB	12	B
10	Am Broch tigten hefle Duncken den woltigen	regnen/**Regen**	JAB	12	A
10	Gannbe hefzu dunkun terken tig Woles len	**regnen**/Regen	NWL	12	B
10	Ten broch Hefgen Tigam dunkti ken woldenle	regnen/**Regen**	NWL	12	A
11	Der Zahnarzt musste bei drei Karieslöchern tief	**bohren**/Bohrer	SENT	13	B
11	Für das Kariesloch brauchte der Zahnarzt einen	bohren/**Bohrer**	SENT	13	A
11	Der Rilö musste bei drei Eszihnkateifchern irzt	**bohren**/Bohrer	JAB	13	A
11	Für das Eszihnkabreuch irzte der Rilech einen	bohren/**Bohrer**	JAB	13	B
11	Moss Rilö Dreichern te zihn esderkateifbei irzt	**bohren**/Bohrer	NWL	13	A
11	Te Nen Esdaskabreuch irztei zihn Rilech förder	bohren/**Bohrer**	NWL	13	B
12	Gewitternd begann es zu blitzen und zu	**donnern**/Donner	SENT	11	A
12	Beim Gewitter sah man Blitze und hörte	donnern/**Donner**	SENT	11	B
12	Gannbeternd witblit es zu gezen und zu	**donnern**/Donner	JAB	11	B
12	Beim Hörgeter blit man Sahze und witte	donnern/**Donner**	JAB	11	A
12	Gannesund zube zen ternd gezu wit blit	**donnern**/Donner	NWL	11	B
12	Ter Hörgebeim Blit Te sahman ze wittund	donnern/**Donner**	NWL	11	A
13	Er wollte das wilde Pferd ohne Sattel	**reiten**/Reiter	SENT	11	B
13	Der Ledersattel war bequem für Pferd und	reiten/**Reiter**	SENT	11	A
13	Er wollte das pfirde Sit ohne Wilttel	**reiten**/Reiter	JAB	11	A
13	Der Quemsaletel pfirt derwar für Be und	reiten/**Reiter**	JAB	11	B
13	Te Teloh wull Pfirter sit nede wildas	**reiten**/Reiter	NWL	11	A
13	Sa Fürundtelder Pfirt derwar quem be le	reiten/**Reiter**	NWL	11	B
14	Beim Ballett sollten alle leichtfüßig zum Musikstück	**tanzen**/Tänzer	SENT	14	A
14	Zu Ballettmusik sah sie einen sehr leichtfüßigen	tanzen/**Tänzer**	SENT	14	B
14	Beim Leiftfü sollten alle mubaßig zum Stäcklettsik	**tanzen**/Tänzer	JAB	14	B

Item sex-tett	Normal sentences (SENT), jabberwocky sentences (JAB), and non-word lists (NWL)	Target word	Condition	Syllable count	Item set
14	Zu Leiftsahsahrlett sik sie einen fü mubaßigen	tanzen/**Tänzer**	JAB	14	A
14	Sill Leiftzum Alleßig ten mubabeim fü stäcklettsik	**tanzen**/Tänzer	NWL	14	B
14	Gen leiftsahsahrei Sik nen zußi fü mubasielett	tanzen/**Tänzer**	NWL	14	A
15	Der Soldat musste damals im Krieg erbittert	**kämpfen**/Kämpfer	SENT	12	A
15	Im Krieg wurde der Soldat ein erbitterter	kämpfen/**Kämpfer**	SENT	12	B
15	Der Krauger musste damals im Dat bitsoltert	**kämpfen**/Kämpfer	JAB	12	B
15	Im Dat gerde der Kraugwur ein bitsolterter	kämpfen/**Kämpfer**	JAB	12	A
15	Tert Krauger Malsda mossim te dat bitsolder	**kämpfen**/Kämpfer	NWL	12	B
15	Ter dat Gerim Ter dewur kraug bitsolderein	kämpfen/**Kämpfer**	NWL	12	A
16	Judas plante schon seit langem Jesus zu	**verraten**/Verräter	SENT	11	B
16	Jesus entlarvte Judas schon bald als den	verraten/**Verräter**	SENT	11	A
16	Enling plante schon seit susju Dasje zu	**verraten**/Verräter	JAB	11	A
16	Daldent dasjute Lirvje schon sus als den	verraten/**Verräter**	JAB	11	B
16	Enling Seitzu te sus juplan dasje zon	**verraten**/Verräter	NWL	11	A
16	Dalden dasjezon lirvals te sus Dent ju	verraten/**Verräter**	NWL	11	B
17	Ruhig begann daVinci die Mona Lisa zu	**malen**/Maler	SENT	13	B
17	Mit Mona Lisa übertraf daVinci sich als	malen/**Maler**	SENT	13	A
17	Vinig begann Nalirah die Cimo Sada zu	**malen**/Maler	JAB	13	A
17	Mit Cimo Sada bervinü Nalitrif sich als	malen/**Maler**	JAB	13	B
17	Vinzu Bedie nalirah Ig cimo Sada gann	**malen**/Maler	NWL	13	A
17	Mo cimit Alsda Bersichü nalitrif Sa vin	malen/**Maler**	NWL	13	B
18	Am Swimmingpool musste er auf einem Handtuch	**liegen**/Liege	SENT	12	B
18	Am Pool reservierte ein Handtuch die freie	liegen/**Liege**	SENT	12	A
18	Am Hondpulming musste er auf einem Tachswim	**liegen**/Liege	JAB	12	A
18	Am Hond tachfriepulte ein Revaur die sere	liegen/**Liege**	JAB	12	B
18	Moss Mingpulauf Nemam te hond erein tachswim	**liegen**/Liege	NWL	12	A
18	Te hond Tachdiepulam Re evaur frie serein	liegen/**Liege**	NWL	12	B
19	Jetzt beschloß der Fischer eine Forelle zu	**angeln**/Angel	SENT	12	A
19	Der Fischer hatte eine Forelle an der	angeln/**Angel**	SENT	12	B

Item sextett	Normal sentences (SENT), jabberwocky sentences (JAB), and non-word lists (NWL)	Target word	Condition	Syllable count	Item set
19	Jetzt relfi der Schlefscher eine Befole zu	**angeln**/Angel	JAB	12	B
19	Der Hatscher relte eine Fofile an der	angeln/**Angel**	JAB	12	A
19	Schlef relei fi lezu Nejutzt befoder scher	**angeln**/Angel	NWL	12	B
19	Scher hatei Relder Lene anfider te fo	angeln/**Angel**	NWL	12	A
20	Dieses komplexe Problem war unmöglich einfach zu	**lösen**/Lösung	SENT	14	B
20	Für komplexe Probleme gab es keine einfache	lösen/**Lösung**	SENT	14	A
20	Dieses unproxe Fichein war blemkomlich plemög zu	**lösen**/Lösung	JAB	14	A
20	Für pleproxe Blefame gab es keine komeinche	lösen/**Lösung**	JAB	14	B
20	Lichwar unprozu fichein xe blemkomdie Plemög ses	**lösen**/Lösung	NWL	14	A
20	Xe pleprogab blefafür me che Esne komeinkei	lösen/**Lösung**	NWL	14	B
21	Vom kalten Wind begannen die Augen zu	**tränen**/Träne	SENT	11	B
21	In ihre Augen trieb der Eiswind eine	tränen/**Träne**	SENT	11	A
21	Vom anten Kal begannen die Wondgen zu	**tränen**/Träne	JAB	11	A
21	In ihre Wondgen au der Treubies eine	tränen/**Träne**	JAB	11	B
21	Ten Voman kal enbedie gen Wondzu gann	**tränen**/Träne	NWL	11	A
21	Re Inei genih au wond Treubies neder	tränen/**Träne**	NWL	11	B
22	Ihren besten Freund durfte sie allein platonisch	**lieben**/Liebe	SENT	13	B
22	Zwischen besten Freunden gab es oft platonische	lieben/**Liebe**	SENT	13	A
22	Ihren freintten Bes durfte sie allein toplanisch	**lieben**/Liebe	JAB	13	A
22	Zwischen freintten Besden plin es oft togabische	lieben/**Liebe**	JAB	13	B
22	Tensief freinta bes leinih ren Tenisch toplandurf	**lieben**/Liebe	NWL	13	A
22	Tenden freintes besische plin schen Zwi togaboft	lieben/**Liebe**	NWL	13	B
23	Er begann Kunst und seltene Briefmarken zu	**sammeln**/Sammlung	SENT	12	B
23	Kunst und seltene Briefmarken zählten zu der	sammeln/**Sammlung**	SENT	12	A
23	Er begann Brauf und temarne Kamstselken zu	**sammeln**/Sammlung	JAB	12	A
23	Brauf und marzühlne Kamstselken teten zu der	sammeln/**Sammlung**	JAB	12	B

Item sextett	Normal sentences (SENT), jabberwocky sentences (JAB), and non-word lists (NWL)	Target word	Condition	Syllable count	Item set
23	Ken Erund brauf be temarzu Kamstselne gann	**sammeln**/Sammlung	NWL	12	A
23	Brauf ken tezühlder kamstselzu Marund ne ten	sammeln/**Sammlung**	NWL	12	B
24	Diese Witwen trugen schwarze Kleidung um zu	**trauern**/Trauer	SENT	12	B
24	Die Witwe zeigte mit schwarzer Kleidung ihre	trauern/**Trauer**	SENT	12	A
24	Diese Schwarwen kleigen truze Witdung um zu	**trauern**/Trauer	JAB	12	A
24	Die Schwarwe kleite mit zaugzer Witdung ihre	trauern/**Trauer**	JAB	12	B
24	We Schwardie Klemit zer zaugih witte redung	**trauern**/Trauer	NWL	12	A
24	Dungze schwardie Klese Truzu witum gen wen	trauern/**Trauer**	NWL	12	B
25	Die Sanitäter mussten den Verletzten sehr weit	**tragen**/Trage	SENT	13	A
25	Sanitäter schleppten den Verletzten weit auf der	tragen/**Trage**	SENT	13	B
25	Die Wietsasihrter mussten den Täniten letz ver	**tragen**/Trage	JAB	13	B
25	Wietsaschluppter verten den Täniten letz auf der	tragen/**Trage**	JAB	13	A
25	Ter wietsasihrdie Tenden Ten tänimoss letz ver	**tragen**/Trage	NWL	13	B
25	Wietsaschluppder verauf ten tädenni Letz ten ter	tragen/**Trage**	NWL	13	A
26	Mit Karotten und Heu musste er Hasen	**füttern**/Futter	SENT	11	B
26	Karotten und Heu dienten den Hasen als	füttern/**Futter**	SENT	11	A
26	Mit Hahieten und Ka musste er Rotsen	**füttern**/Futter	JAB	11	A
26	Dienhaten und Ka hieten den Rotsen als	füttern/**Futter**	JAB	11	B
26	Ten Hahiemit Sen ka Tener moss rotund	**füttern**/Futter	NWL	11	A
26	Hadenund Ten ka hiedien sen Rotals ten	füttern/**Futter**	NWL	11	B
27	Nach der Sauna wollte sie keinesfalls kalt	**duschen**/Dusche	SENT	11	B
27	Nach der Sauna brauchte sie eine kalte	duschen/**Dusche**	SENT	11	A
27	Nach der Keltseu wollte sie fallsnesna kei	**duschen**/Dusche	JAB	11	A
27	Nach der Breuchkal nate sie eine seute	duschen/**Dusche**	JAB	11	B
27	Te wull keltsie dernach seu Fallsnesna kei	**duschen**/Dusche	NWL	11	A
27	Te breuch nakal nachei te Derne seusie	duschen/**Dusche**	NWL	11	B
28	Sie wollte die Ostereier leuchtend und knallbunt	**färben**/Farbe	SENT	13	A
28	Sie malten die Ostereier bunt mit leuchtender	färben/**Farbe**	SENT	13	B

Item sex-tett	Normal sentences (SENT), jabberwocky sentences (JAB), and non-word lists (NWL)	Target word	Condition	Syllable count	Item set
28	Sie wollte die Liechbuntoser knilltend und terei	**färben**/Farbe	JAB	13	B
28	Sie terten die Eibuntoser liech mit tenmalder	färben/**Farbe**	JAB	13	A
28	Tend serund wull liechbuntossie Knilldie te terei	**färben**/Farbe	NWL	13	B
28	Ten erdie ter eibuntosmit Liech ten maldersie	färben/**Farbe**	NWL	13	A
29	Um Meister zu werden musste er jahrelang	**üben**/Übung	SENT	12	A
29	Um Meister zu werden braucht es jahrelange	üben/**Übung**	SENT	12	B
29	Um Jahter zu langden musste er werremeis	**üben**/Übung	JAB	12	B
29	Um Jater zu langden meis es werrebreuchte	üben/**Übung**	JAB	12	A
29	Ter jahum Te langzu dener moss werremeis	**üben**/Übung	NWL	12	B
29	Ter denbreucht Jah langzu meis re esewerum	üben/**Übung**	NWL	12	A
30	Wegen der Vitamine sollte man Äpfel nicht	**schälen**/Schale	SENT	13	B
30	Vitamine liegen beim Apfel gleich unter der	schälen/**Schale**	SENT	13	A
30	Wegen der Miaptane sollte man Felvi nicht	**schälen**/Schale	JAB	13	A
30	Milietane apgen beim Felvi gleich unter der	schälen/**Schale**	JAB	13	B
30	Mander We miaptanicht sullne gen Felvi te	**schälen**/Schale	NWL	13	A
30	Milietanbeum apun gen felvi Ter neder gliech	schälen/**Schale**	NWL	13	B

6.1.3 PROJECT 3: PREDICTING WORDS AND SEMANTIC CATEGORIES

Table 6-3. Stimulus set for project SEMTRACK (investigating word and semantic word category prediction). 1-7, word sequence; 2, semantics without syntax; 3, non-word lists); Item set, participants were exposed to either item set A or B; Nr, stimulus number in item set; T1-T2, possible target words (T2 target words are considered semantically correct).

NR	Set	Word sequence	T1	T2
1	A	Am Strand liegen Menschen die sich stundenlang	erfrieren	**sonnen**
1	B	In den Ferien gehen die braungebrannten Wasserratten	zittern	**schwimmen**
2	A	In brütender Hitze droht leckeres Speiseeis zu	frieren	**schmelzen**
2	B	An heißen Ferientagen gingen alle im See	frieren	**baden**
3	A	Bei heißen Temperaturen bekommen Schüler und Lehrer	Kerzen	**Hitzefrei**
3	B	Wegen der Hitze musste er die Gartenpflanzen	ausrutschen	**gießen**
4	A	Badebecken unter freiem Himmel findet man im	Weihnachtsbaum	**Freibad**
4	B	Bei Sonnenschein kann man sich mit Bier	aufwärmen	**erfrischen**
5	A	Wegen der Hitze trage ich statt Turnschuhen	Eisschollen	**Sandalen**
5	B	Statt einem Badeanzug tragen viele Frauen einen	Weihnachtsbaum	**Bikini**
6	A	Auf der Blumenwiese wollen wir mit Kuchen	rodeln	**picknicken**
6	B	Männer tragen im Freibad gern nur eine	Piste	**Badehose**
7	A	Kaum sind die Wolken verzogen herrscht strahlender	Tee	**Sonnenschein**
7	B	Mit buntem Sandspielzeug fahren wir hinaus ans	Winterfell	**Meer**
8	A	Männer tragen Badehosen Frauen tragen einen geschlossenen	Eiszapfen	**Badeanzug**
8	B	Beim Picknick sitzen auf Marmeladenbrötchen gern summende	Handschuhe	**Bienen**
9	A	Das rothaarige Mädchen bekommt bei Sonnenschein viele	Handschuhe	**Sommersprossen**
9	B	In der sengenden Mittagssonne kann Haut leicht	rodeln	**verbrennen**
10	A	Mit seinem Surfbrett geht er im Meer	ausrutschen	**surfen**
10	B	Eistee und andere kalte Limonaden sind wohltuende	Adventskalender	**Erfrischungen**
11	A	Obst und Picknickdecke packe ich in den	Weihnachtsbaumschmuck	**Picknickkorb**
11	B	Unbeabsichtigte Funken führen in vertrockneten Wäldchen zum	Winterfell	**Waldbrand**
12	A	Zu Sandalen trage ich einen besonders kurzen	Adventskalender	**Minirock**
12	B	Am Strand baue ich mit Sand eine	Rute	**Sandburg**
13	A	Das beste Schokoeis verkauft das kleine italienische	Feuerwerk	**Eiscafe**
13	B	Am Himmel über dem Freibad scheint die	Sauna	**Sonne**
14	A	Auf dem sonnigen Feld gedeiht das goldene	Weihnachtslied	**Getreide**
14	B	Gegen biestige Mücken hilft nur ein gutes	Weihnachtslied	**Mückenspray**

NR	Set	Word sequence	T1	T2
15	A	Bei Hitze trinke ich um nicht zu	zittern	**verdursten**
15	B	Ich kratze am nackten Bein meinen juckenden	Weihnachts-baumschmuck	**Mückenstich**
1	A	He dei Ferien dengen ni Sonnenbräune Wasserratte	erfrieren	**schwimmen**
1	B	Mie Strand asgen Menschenschar Dei lich Stunden	Lift	**sonnen**
2	A	Ga Bruthitze Ferientag imal genle nin See	Winterfell	**baden**
2	B	Rohd Brüten Hitze zut Leckerei Speiseeis niden	ausrutschen	**schmelzen**
3	A	Dieste sum Hitze gener re wed Gartenpflanze	Iglu	**gießen**
3	B	Deb Hitze Temperatur unbeimen Schüler kom Lehrerschaft	zittern	**Hitzefrei**
4	A	Nak Sonnenschein eimb sim nan tich Bier	Rute	**erfrischen**
4	B	Badebecken imman Freiheit Himmel terdet ni nuf	Plätzchen	**Freibad**
5	A	Nem genei Badeanzug stranen Vielzahl Frau neitatte	Schneeschippe	**Bikini**
5	B	Derge ra Hitze tattich te genw Turnschuhe	Schneeschippe	**Sandalen**
6	A	Mann eintrare min Freibad reg ne genur	Skispringen	**Badehose**
6	B	Umt dei Blumenwiese wiraf rol nelw Kuchen	Skispringen	**picknicken**
7	A	Tah Farbe Sandspielzeug wirhin maf reinans su	Schnee-ballschlacht	**Meer**
7	B	Dierscht geinde ves Wolke umkaherr zond Strahlen	Weihnachts-baumschmuck	**Sonnenschein**
8	A	Gede Picknick fautzen meib Marmeladenbrötchen sirn Summen	Sauna	**Bienen**
8	B	Mann nentra Badehose Frau gentrane geneire Geschlossenheit	Feuerwerk	**Badeanzug**
9	A	Re kanen Sengen Mittagssonne deil Haut nincht	Handschuhe	**verbrennen**
9	B	Kob Rothaarigkeit Mädchen dabeimmt se Sonnenschein Menge	Iglu	**Sommer-sprossen**
10	A	Eistee nuden nasie Kälte Limonade derend Wohltat	aufwärmen	**Erfrischungen**
10	B	Tei mige Surfbrett nihrt me sem Meer	Schal	**surfen**
11	A	Unabsicht Funken inren zuh Trockenheit Waldgebiet füm	Eisschollen	**Waldbrand**
11	B	Obst pan Picknickdecke ickech nud ne di	Eisschollen	**Picknickkorb**
12	A	Mei Strand imit beu na Sand echa	Lift	**Sandburg**
12	B	Trai Sandalen zunen ech gei Besonderheit Kürze	Kerzen	**Minirock**
13	A	Üd Himmel amschei emb Freibad tiend re	Ski	**Sonne**
13	B	Ver Qualität Schokoeis dadast fakus Kleinheit Italien	Weihnachtslied	**Eiscafe**
14	A	Ihine Biest Mücke gelneft ner gu Güte	Eiszapfen	**Mückenspray**
14	B	Fes gaugie Sonne Feld dademt deihene Gold	Winterzeit	**Getreide**
15	A	Kra amime ne Nacktheit Bein ichtzen Jucken	Weihnachtsbaum	**Mückenstich**
15	B	Tri Hitze umni eib kech nuch itz	Eiszapfen	**verdursten**
1	A	He dei Warsibräu dengen ni Ensofennen Enseratter	Sauna	**schwimmen**

NR	Set	Word sequence	T1	T2
1	B	Mie Dannsten asgen Strunsch Dei lich Medenschar	Winterzeit	**sonnen**
2	A	Ga Ferebrut Seziheiten imal genle nin Gat	Ski	**baden**
2	B	Rohd Hitten Brüse zut Speizerei Eckelsei niden	frieren	**schmelzen**
3	A	Dieste sum Garnze gener re wed Hittenpflazen	Schneeballschlacht	**gießen**
3	B	Deb Schütemp Turlerschaft unbeimen Lehze kom Hiterarer	Kerzen	**Hitzefrei**
4	A	Nak Biescheinne eimb sim nan tich Ronns	Iglu	**erfrischen**
4	B	Himfreidene imman Beckheit Bamel terdet ni nuf	Piste	**Freibad**
5	A	Nem genei Fraubaviel stranen Naguzah Delz neitatte	Schneeschippe	**Bikini**
5	B	Derge ra Schutih tattich te genw Heturnzen	Winterfell	**Sandalen**
6	A	Freinn eintrare min Mabad reg ne genur	Rute	**Badehose**
6	B	Umt dei Ulbchen wiraf rol nelw Kuwiemense	Schneeballschlacht	**picknicken**
7	A	Tah Farsandzeug Spiebel wirhin maf reinans su	Weihnachtsbaum	**Meer**
7	B	Dierscht geinde ves Westra umkaherr zond Lohlenk	Weihnachtsbaum	**Sonnenschein**
8	A	Ge Mardenbrömt fautzen meib Nicklasummede sirn Nepickchen	Plätzchen	**Bienen**
8	B	Gam nentra Fraschlosenba Honn gentrane geneire Heiteusede	Plätzchen	**Badeanzug**
9	A	Re kanen Sonha Mitsenggatsen deil Neut nincht	Schal	**verbrennen**
9	B	Kob Scheinsomädge Hanneinchen dabeimmt se Mennkeit Gartor	Schal	**Sommersprossen**
10	A	Letat nuden nasie Mosei Wohlkäldane derend Teite	Winterzeit	**Erfrischungen**
10	B	Tei mige Burfstret nihrt me sem Reem	Adventskalender	**surfen**
11	A	Befuntrockwanukeit Kenheit inren zuh Tabgeschiet Giblined füm	Piste	**Waldbrand**
11	B	Spick pan Deckbonicket ickech nud ne di	erfrieren	**Picknickkorb**
12	A	Mei Dranst imit beu na Dans echa	aufwärmen	**Sandburg**
12	B	Trai Dasonkür zunen ech gei Sanleheitze Neberd	Ski	**Minirock**
13	A	Üd Freimel amschei emb Himbad tiend re	rodeln	**Sonne**
13	B	Ver Kleinscholi Kotäsei dadast fauks Taquaheit Tiline	Skispringen	**Eiscafe**
14	A	Ihine Müst Tüge gelneft ner gu Biecke	Tee	**Mückenspray**
14	B	Fes gaugie Nefe Lodd dademt deihene Solng	Tee	**Getreide**
15	A	Kra amime ne Junnack Eick ichtzen Bentheit	Feuerwerk	**Mückenstich**
15	B	Tri Zetih umni eib kech nuch itz	Lift	**verdursten**
1	A	Bei Eiseskälte geht sie in die finnische	Sommersprossen	**Sauna**
1	B	Meine unterkühlten Muskeln beginnen wie Espenlaub zu	baden	**zittern**
2	A	In den schneebedeckten Bergen fahre ich gern	Eiscafe	**Ski**
2	B	Nachts benutzen wir eine Wärmflasche wenn wir	surfen	**frieren**

NR	Set	Word sequence	T1	T2
3	A	Gegen frierende Hände im Wind trägt er	Hitzefrei	**Handschuhe**
3	B	Am Baum brennen an Weihnachten viele helle	Bienen	**Kerzen**
4	A	Die Kinder veranstalten im ersten Schnee eine	Badehose	**Schneeballschlacht**
4	B	Zu Weihnachten schlagen wir im Wald einen	Badeanzug	**Weihnachtsbaum**
5	A	An Heiligabend brennen leuchtende Kerzen am hochgewachsenen	Picknickkorb	**Weihnachtsbaum**
5	B	Im Dezember öffnet man täglich Türchen im	Waldbrand	**Adventskalender**
6	A	An der vereisten Regenrinne hängen glitzernde lange	Sandalen	**Eiszapfen**
6	B	Unterm Weihnachtsbaum singt die Familie ein traditionelles	Eiscafe	**Weihnachtslied**
7	A	Am Berg jauchzen Kinder auf Schlitten beim	schmelzen	**rodeln**
7	B	Im Advent bäckt die Mutter frische warme	Sandalen	**Plätzchen**
8	A	Nach einem Winterspaziergang muss man sich drinnen	gießen	**aufwärmen**
8	B	Auf einer zugefrorenen Pfütze kann man ausversehen	verbrennen	**ausrutschen**
9	A	Bei frostigem Wetter trinkt er gern heißen	Minirock	**Tee**
9	B	Beim Rodeln braucht man Handschuhe Mütze und	Getreide	**Schal**
10	A	Das Schneehaus des Eskimos nennt man auch	Sonnenschein	**Iglu**
10	B	Die Uhren werden im November umgestellt auf	Bikini	**Winterzeit**
11	A	Im Januar schippe ich Schnee mit der	Sandburg	**Schneeschippe**
11	B	Tiere überleben die kalte Jahreszeit durch ihr	Mückenspray	**Winterfell**
12	A	Unartige Kinder bestraft Knecht Ruprecht mit der	Sonne	**Rute**
12	B	Mit seinem Snowboard geht er auf die	Sommersprossen	**Piste**
13	A	An Silvester veranstalten wir immer ein knallendes	Getreide	**Feuerwerk**
13	B	Auf den Berg nehmen Skifahrer gern den	Mückenstich	**Lift**
14	A	Menschen ohne Kleidung werden im erbarmungslosen Eiswind	picknicken	**erfrieren**
14	B	Viele Menschen benutzen Strohsterne und Lametta als	Erfrischungen	**Weihnachtsbaumschmuck**
15	A	In der Arktis vor Grönland treiben riesige	Bienen	**Eisschollen**
15	B	Die olympische Sportart an der Skischanze heißt	Badehose	**Skispringen**
1	A	Wiemei Unterkühlung Muskel zunen gine Espenlaub eb	schmelzen	**zittern**
1	B	Gein Eiseskälte bie Frau de tih Finnland	Waldbrand	**Sauna**
2	A	Nacht niwutzen wern birwe Wärmflasche ne nei	surfen	**frieren**
2	B	Ni fah Schneedecke Berg dener chi Vorliebe	Hitzefrei	**Ski**
3	A	Vie Baum annen bren Weihnachten lema Helligkeit	baden	**Kerzen**
3	B	Ergen Frieren Hand tärde Wind gimde teg	Mückenspray	**Handschuhe**
4	A	Mi Weihnachten gennen wa schlir Wald eizu	sonnen	**Weihnachtsbaum**

NR	Set	Word sequence	T1	T2
4	B	Dei Kind aneinten mie Erstmaligkeit Schnee stalver	Minirock	**Schneeballschlacht**
5	A	Milich Dezember mannet öff Tag Tür michen	Freibad	**Adventskalender**
5	B	Ner Heiligabend maben Leuchten Kerze nande Hochgewachsenheit	schwimmen	**Weihnachtsbaum**
6	A	Singun Weihnachtsbaum termt nedei Familie neiles Tradition	Mückenspray	**Weihnachtslied**
6	B	Nede vernagte Eis Regenrinne derhän Glitzern Länge	schwimmen	**Eiszapfen**
7	A	Mi Advent biet däck Mutter Frische Wärme	Hitzefrei	**Plätzchen**
7	B	Jau Berg meichen Kind fauber Schlitten zam	verdursten	**rodeln**
8	A	Nau maner Gefrorensein Pfütze zuneik nafaus Versehen	Mückenstich	**ausrutschen**
8	B	Eich mansi Winterspaziergang sum nem schan Innenraum	erfrischen	**aufwärmen**
9	A	Deim Rodeln unchte barb Handschuh Mütze naum	Badeanzug	**Schal**
9	B	Ger Frost Wetter ernkt eib trin Schokolade	Sandburg	**Tee**
10	A	Ram Uhr deiden efin November Umstellung weu	verdursten	**Winterzeit**
10	B	Aum Schneehaus sen Eskimo neds anch dant	verbrennen	**Iglu**
11	A	Tier berdiedule ürche Kälte Jahreszeit rih neb	picknicken	**Winterfell**
11	B	De Januar mitschip re Schnee pich mi	Meer	**Schneeschippe**
12	A	Sim diege Snowboard tei ehmt nauf re	Waldbrand	**Piste**
12	B	Unartigkeit Kind mistrate Knecht Ruprecht reb deft	Sonne	**Rute**
13	A	Neh ner Berg menden Skifahrer fnau deg	Sandalen	**Lift**
13	B	Lir Silvester imanetinen werm sta veran Knall	Badehose	**Feuerwerk**
14	A	Vielzahl Mensch nundalsen Strohstern ebe Lametta utzen	sonnen	**Weihnachtsbaumschmuck**
14	B	Mensch denne Kleidung werho mi Erbarmungslosigkeit Eiswind	gießen	**erfrieren**
15	A	Dei Olympia Sportart na deih Skischanze reßt	Getreide	**Skispringen**
15	B	Ve ror Arktis tride Grönland inben Größe	Picknickkorb	**Eisschollen**
1	A	Wiemei Lubkühsaune Terlung zunen gine Penkelmus eb	Freibad	**zittern**
1	B	Gein Faukälfises bie Tern de tih Lanedin	Bienen	**Sauna**
2	A	Schrecht niwutzen wern birwe Flawänam ne nei	Sonnenschein	**frieren**
2	B	Ni fah Vorbiechle Gensch denre rei Debecke	baden	**Ski**
3	A	Vie Weuhl annen bren Bamichkeit lema Nateihleng	Badeanzug	**Kerzen**
3	B	Ergen Hawirn Freid tärde Nend gimde teg	gießen	**Handschuhe**
4	A	Mi Tehnwanach gennen wa schlir Weild eizu	Sommersprossen	**Weihnachtsbaum**
4	B	Dei Nenscht aneinten mei Keikiesemad Trilg stalver	erfrischen	**Schneeballschlacht**
5	A	Milich Tatürem mannet öff Gerb Zed michen	surfen	**Adventskalender**
5	B	Ner Leuhokerheit maben Wachshei Gezech nande Tenalichkenbend	Bikini	**Weihnachtsbaum**

NR	Set	Word sequence	T1	T2
6	A	Singun Fatration termt nedei Miweihnabat nei Schumdilie	Picknickkorb	**Weihnachtslied**
6	B	Nede vernagte Rin Gliseinegen derhän Retzge Länern	Meer	**Eiszapfen**
7	A	Mi Frimu biet däck Attsche Venter Mewärd	Minirock	**Plätzchen**
7	B	Jau Tschlit meichen Kirg fauber Benden zam	Erfrischungen	**rodeln**
8	A	Nau maner Seipfüverseh Nentze zuneik nafaus Frogerne	Eiscafe	**ausrutschen**
8	B	Eich mansi Rauwispanemtern sum nem schan Zirnganing	Sandburg	**aufwärmen**
9	A	Deim Müschuh uncht barb Hantze Delornde naum	verdursten	**Schal**
9	B	Ger Wetsch Froko ernkt eib trin Ostterdale	Sonne	**Tee**
10	A	Ram Verm deiden efin Uhnostelg Lunumber weu	schwimmen	**Winterzeit**
10	B	Aum Kihaumosch sen Nesees neds anch dant	Mückenstich	**Iglu**
11	A	Res berdiedule ürche Kätiert Zeijahtel rih neb	erfrischen	**Winterfell**
11	B	De Renaja mitschip re Neusch pich mi	sonnen	**Schneeschippe**
12	A	Sim diege Warboonds tei ehmt nauf re	Bikini	**Piste**
12	B	Nukindartrecht Teik mistrate Gink Purtech reb deft	schmelzen	**Rute**
13	A	Neh ner Bekisrer menden Fahrg fnau deg	Meer	**Lift**
13	B	Lir Tersil imanetinen werm sta veran Vesknall	Freibad	**Feuerwerk**
14	A	Zalstroh Tansch nundalsen Vielstehr ebe Mentmela utzen	verbrennen	**Weihnachtsbaumschmuck**
14	B	Barm denne Lonschernd werho mi Mekleiwisig Dungiesungskeit	picknicken	**erfrieren**
15	A	Dei Artschanpiaze Kilymps na deih Portso reßt	Erfrischungen	**Skispringen**
15	B	Ve ror Landtis tride Kaßer inben Grögrön	Sonnenschein	**Eisschollen**

6.2 QUESTIONNAIRES / TEST SHEETS

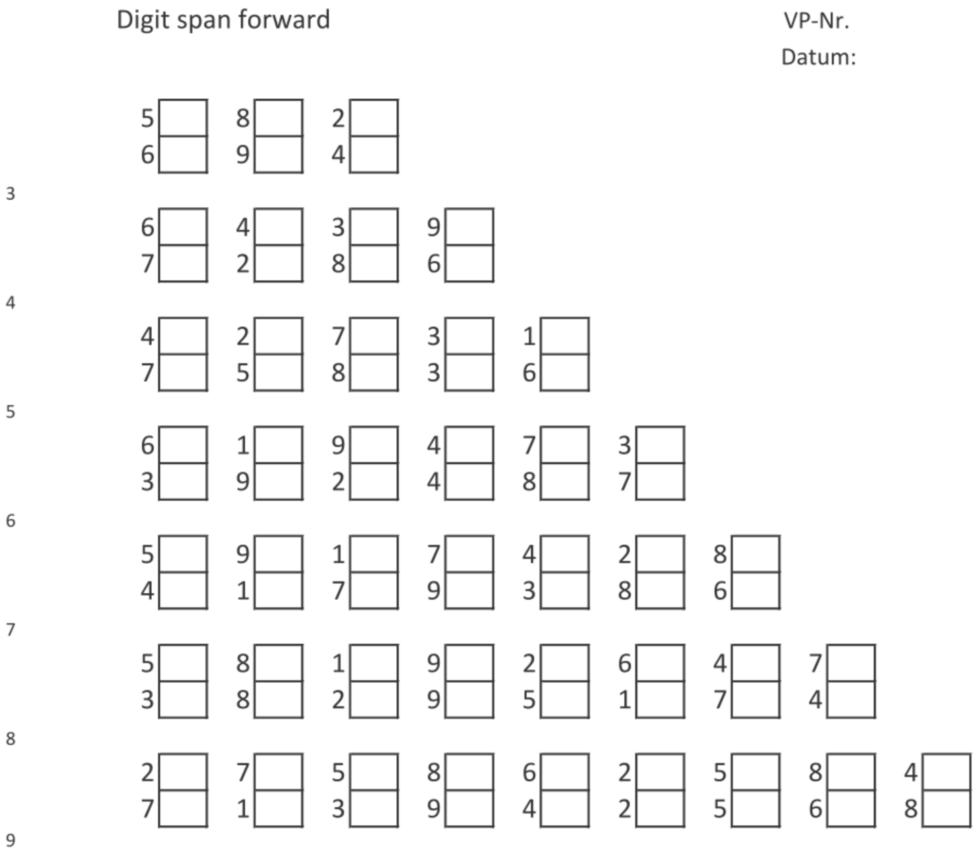
6.2.1 GENERAL AND CURRENT LIFESTYLE HABITS

Nr	Frage	Antwort(-optionen)
1	Versuchspersonennummer	______________
2	Alter	______________
3	Geschlecht	______________
4	Welchen Beruf/welches Studium üben Sie aus?	______________
5	Höchster akademischer Grad:	☐ Hauptschulabschluss ☐ Realschulabschluss ☐ Abitur ☐ Bachelor/Vordiplom ☐ Master/Diplom/Magister ☐ Promotion/PhD ☐ Andere: ___________
6a	Wie gut haben Sie in der vergangenen Nacht geschlafen?	☐ sehr schlecht ☐ schlecht ☐ mittel ☐ gut ☐ sehr gut
6b	Wie viele Stunden haben Sie in der letzten Nacht geschlafen? (in Stunden)	_________
7a	Trinken Sie regelmäßig Alkohol?	☐ ja ☐ nein
7b	Wenn „ja“: Wie oft trinken Sie durchschnittlich in der Woche Alkohol?	_________
7c	Wovon trinken Sie wie viel? (in Gläsern)	Wein _________ Bier _________ Schnaps _________ Sonstiges _________
7d	Haben Sie in den vergangenen 24 Stunden Alkohol zu sich genommen?	☐ ja ☐ nein

7e	Wenn „ja“: Wovon haben Sie wie viel getrunken?	Wein ________ Bier ________ Schnaps ________ Sonstiges ________
8a	Trinken Sie täglich koffeinhaltige Getränke? (Kaffee, Tee, Cola, Energy drinks)	☐ ja ☐ nein
8b	Wenn „ja“: Wie viel trinken Sie durchschnittlich am Tag?	Kaffee _________ Tee _________ Cola _________ Energy drinks _______ Sonstiges _________
8c	Haben Sie heute schon koffeinhaltige Getränke zu sich genommen?	☐ ja ☐ nein
8d	Wenn „ja“: Wovon haben Sie wie viel getrunken? (in Tassen/Gläsern)	Kaffee _________ Tee _________ Cola _________ Energy drinks _______ Sonstiges _________
8e	Wenn „ja“: Wie lange ist das her? (in Stunden)	__________
9a	Rauchen Sie?	☐ ja ☐ nein
9b	Wenn „ja“: Wie viele Zigaretten rauchen Sie am Tag?	__________
9c	Haben Sie heute schon geraucht?	☐ ja ☐ nein
9d	Wenn „ja“: Wie viele Zigaretten haben Sie heute schon geraucht?	__________
9e	Wenn „ja“: Vor wie vielen Stunden haben Sie die letzte Zigarette geraucht?	__________

6.2.2 DIGIT SPAN

To ensure that participants in general were able to recall at least six items in a working memory task, only participants correctly remembering six or more items in the Digit Span test (adapted version of the Digit Span Test originally included in the Wechsler Adult Intelligence Scale by David Wechsler, 1955) were invited for fMRI measurements. To guarantee equal conditions for all participants, an electronic version of the digit span was used: Prerecorded digits were played in an automatized way with standardized timing. The participants were asked to listen and repeat the digit sequence either in the original or in the reverse order (i.e., forward and backward digit span, respectively). By increasing the number of digits to remember until the participants failed two times in a row, the individual working memory capacities were estimated. Notably, although both forward and backward digit span were assessed, the cut-off criterion of six items was based on the forward digit span (i.e., analogous to the retention of words in their sequential order in the present study). The following test sheets illustrate the digit sequences:



Digit span forward

VP-Nr.
Datum:

	5 ☐	8 ☐	2 ☐						
3	6 ☐	9 ☐	4 ☐						
	6 ☐	4 ☐	3 ☐	9 ☐					
4	7 ☐	2 ☐	8 ☐	6 ☐					
	4 ☐	2 ☐	7 ☐	3 ☐	1 ☐				
5	7 ☐	5 ☐	8 ☐	3 ☐	6 ☐				
	6 ☐	1 ☐	9 ☐	4 ☐	7 ☐	3 ☐			
6	3 ☐	9 ☐	2 ☐	4 ☐	8 ☐	7 ☐			
	5 ☐	9 ☐	1 ☐	7 ☐	4 ☐	2 ☐	8 ☐		
7	4 ☐	1 ☐	7 ☐	9 ☐	3 ☐	8 ☐	6 ☐		
	5 ☐	8 ☐	1 ☐	9 ☐	2 ☐	6 ☐	4 ☐	7 ☐	
8	3 ☐	8 ☐	2 ☐	9 ☐	5 ☐	1 ☐	7 ☐	4 ☐	
	2 ☐	7 ☐	5 ☐	8 ☐	6 ☐	2 ☐	5 ☐	8 ☐	4 ☐
9	7 ☐	1 ☐	3 ☐	9 ☐	4 ☐	2 ☐	5 ☐	6 ☐	8 ☐

Digit span backward

VP-Nr.
Datum:

4 ☐ 2 ☐
8 ☐ 5 ☐

2

9 ☐ 2 ☐ 6 ☐
5 ☐ 1 ☐ 4 ☐

3

9 ☐ 7 ☐ 2 ☐ 3 ☐
8 ☐ 6 ☐ 9 ☐ 4 ☐

4

6 ☐ 8 ☐ 2 ☐ 5 ☐ 1 ☐
3 ☐ 4 ☐ 8 ☐ 1 ☐ 6 ☐

5

8 ☐ 1 ☐ 4 ☐ 9 ☐ 3 ☐ 5 ☐
6 ☐ 5 ☐ 8 ☐ 4 ☐ 2 ☐ 7 ☐

6

5 ☐ 6 ☐ 3 ☐ 9 ☐ 2 ☐ 1 ☐ 8 ☐
8 ☐ 2 ☐ 1 ☐ 9 ☐ 3 ☐ 7 ☐ 4 ☐

7

8 ☐ 5 ☐ 2 ☐ 6 ☐ 7 ☐ 3 ☐ 4 ☐ 9 ☐
3 ☐ 5 ☐ 6 ☐ 9 ☐ 1 ☐ 8 ☐ 2 ☐ 7 ☐

8

LIST OF PUBLICATIONS

Publications

Manuscript	**Bonhage, C. E.**, Mueller, J. L., Friederici, A. D., & Fiebach, C. J. (2015, in press). Combined eye tracking and fMRI reveals neural basis of linguistic predictions during sentence comprehension, *Cortex*, http://dx.doi.org/10.1016/j.cortex.2015.04.011.
Manuscript	Weber, F., **Bonhage, C. E.,** Exner, C.; Kanske, P. (under review). "Thinking about Thinking": Neural mechanisms and effects on memory.
Book chapter	Mueller, J. L. & **Bonhage, C. E**. (accepted). Wie kommt der Mensch zum Wort? Psycho- und neurolinguistische Untersuchungen zur Verarbeitung und zum Erwerb von Wörtern und deren Bedeutungen.
2014	**Bonhage, C. E.**, Fiebach, C. J., Bahlmann, J., & Mueller, J. L. (2014). Brain signature of working memory for sentence structure: Enriched encoding and facilitated maintenance. *Journal of Cognitive Neuroscience*, 26(8), 1654-1671. doi: 10.1162/jocn_a_00566
2013	Koelsch, S., Skouras, S., Fritz, T., Herrera, P., **Bonhage, C. E.**, Kussner, M. B., & Jacobs, A. M. (2013). The roles of superficial amygdala and auditory cortex in music-evoked fear and joy. *Neuroimage*, 81, 49-60. doi: 10.1016/j.neuroimage.2013.05.008
2009	**Bonhage, C. E.** (2009). Zuneigung-Wärme: Induktion und psychophysiologische Effekte. Diploma Thesis.

Posters

2013	**Bonhage, C. E.**, Mueller, J. L., Friederici, A. D., & Fiebach, C. J. (2013). Predictions during sentence comprehension: A combined eye tracking and fMRI study. Poster presented at 3rd IMPRS NeuroCom Summer School, Leipzig, Germany.
2012	**Bonhage, C. E.**, Brodt, S. B., Schroeter, B. D., Friederici, A. D., & Mueller, J. L. (2012). Syntactic prediction reflected in eye movements. Poster presented at Brainhack 2012, Leipzig, Germany.
	Bonhage, C. E., Fiebach, C. J., Friederici, A. D., Bahlmann, J., & Mueller, J. L. (2012). Syntactic contributions to working memory: A neural basis of the sentence superiority effect. Poster presented at OHBM Conference 2012, Beijing, China.

2011	**Bonhage, C. E.**, Fiebach, C. J., Friederici, A. D., Bahlmann, J., & Mueller, J. L. (2011). Syntactic contributions to working memory: A behavioral study. Poster presented at IMPRS Neurocom & UCL summer school, London, United Kingdom.
2009	**Bonhage, C. E.**, Burgdorf, C., & Stemmler, G. (2009). Personality, Emotion, Feelings & Physiology: How personality moderates the effect of social inclusion / exclusion on physiology and feelings. Poster presented at Society for Psychophysiological Research, 49th Annual Meeting, Berlin.

Talks	
2015	**Bonhage, C. E.** (2015). Anticipating words and word categories during reading: Extracting the neural substrates of predictive linguistic processes via combined fMRI and eye tracking. Talk presented at TEAP 2015, Hildesheim, Germany.
2013	**Bonhage, C. E.** (2011). Ich weiß schon, was du sagen wirst – wenn das Gehirn vorhersagt. Talk presented at the Colloquium of the Neurocognitive Psychology Department, Goethe University of Frankfurt, Germany.
2011	**Bonhage, C. E.** (2011). Syntactic contributions to working memory: an fMRI study. Talk presented at the Colloquium of the Neurocognitive Psychology Department, Goethe University of Frankfurt, Germany.
2009	Stemmler, G., & **Bonhage, C. E.** (2009). Cardiovascular effects of warmth-liking. Talk presented at Society for Psychophysiological Research, 49th Annual Meeting. Berlin. 2009-10-21 - 2009-10-24.

EIGENSTÄNDIGKEITSERKLÄRUNG

Hiermit erkläre ich, Corinna E. Bonhage, dass ich die vorliegende Arbeit ohne die Nutzung anderer als der angegebenen Hilfsmittel und ohne unzulässige Hilfe angefertigt habe; Gedanken, die direkt oder indirekt aus fremden Quellen in die vorliegende Arbeit eingingen, sind als solche im Text kenntlich gemacht worden.

Bei der Konzeption der Experimente, der Auswahl des Stimulusmaterials, der Datenanalyse sowie der Erstellung der Manuskripte wurde ich durch meine Betreuer Jutta L. Mueller, Angela D. Friederici und Christian J. Fiebach beraten; die Anteile aller Co-Autoren an den Manuskripten sind gesondert beschrieben. An der geistigen Erstellung dieser Arbeit waren keinerlei weitere Personen beteiligt. Ebenso hat niemand unmittelbar oder mittelbar geldwerte Leistungen für Arbeiten im Zusammenhang mit dem Inhalt der vorliegenden Dissertation erhalten.

Ich versichere hiermit weiterhin, dass die alleinige Autorschaft der monographisch hinzugefügten Kapitel 1, 2 und 5 bei mir liegt; die Auswahl des Stimulusmaterials sowie die experimentellen Designs für alle in Kapitel 2 beschriebenen Pilotstudien sind in Absprache mit meinen Betreuern Jutta L. Mueller, Christian J. Fiebach, und Angela D. Friederici entstanden.

Zuletzt versichere ich, dass ich die vorlegte Arbeit weder in dieser, noch in ähnlicher Form an einer anderen Universität als Dissertation (oder jegliche andere Art der Prüfungsleistung) vorgelegt oder veröffentlich habe.

Frühere erfolglose Promotionsversuche haben nicht stattgefunden.

Corinna Bonhage

Leipzig, den 14. Dezember 2014

BIBLIOGRAPHISCHE DARSTELLUNG

Corinna E. Bonhage

Memory and prediction in sentence processing – Evidence from behavioral performance, eye tracking, and brain imaging

Fakultät für Biowissenschaften, Pharmazie und Psychologie

Universität Leipzig

Dissertation

139 Seiten, 217 Literaturangaben, 19 Abbildungen, 12 Tabellen

The present thesis aimed at identifying the neural substrate of the facilitatory effect of sentence structure on memory and prediction processes in language. In the first part, the neural basis of the sentence superiority effect was investigated (i.e., the phenomenon that humans are able to recall a larger number of words correctly, if those words are presented in grammatically correct order), demonstrating that sentence structure indeed helps to compensate for increasing set sizes of memoranda: Overall, sentence structure led to observable benefits for behavioral working memory performance and was reflected in a two-fold neural pattern of increased encoding and decreased maintenance brain activity. In contrast to ungrammatical word sequences, sentences with low and high working memory load were recalled equally accurate and with comparable neural effort. Additionally, remembering sentences did not depend on rehearsal strategies – behavioral performance and functional magnetic resonance imaging (fMRI) data suggested that in contrast to ungrammatical word sequences, sentences are recalled equally accurate with or without rehearsal and with a comparable neural effort in Broca's area.

In addition to memorizing previous input, humans accelerate linguistic processing by predicting upcoming elements online. In the second part of the thesis anticipatory processes in language are demonstrated via a new 'predictive eye-gaze reading task' conducted in the magnetic resonance scanner. Brain imaging data reveal that word category predictions are supported by ventral premotor cortex, hippocampus, and basal ganglia, whereas the anticipation of reading a specific word in a highly constrained sentence resulted in enhanced engagement of the semantic brain network as well as secondary visual areas.

As predictions are generated based on prior experiences stored in memory, memorizing sentences and predicting upcoming syntactic elements are indigenously linked and were assumed to draw on (partly) overlapping neural resources. A combined analysis of areas involved in working memory encoding of sentence fragments and word category prediction provides first evidence for a shared brain system for memory and prediction, consisting of hippocampus, thalamus/putamen, and angular gyrus.

Nachweis über Anteile der Co-Autoren:

Titel: **Brain Signature of Working Memory for Sentence Structure: Enriched Encoding and Facilitated Maintenance**

Journal: Journal of Cognitive Neuroscience

Autoren: Bonhage, C. E., Fiebach, C. J., Bahlmann, J., & Mueller, J. L.

Anteil Corinna E. Bonhage:

- Konzeption/Operationalisierung
- Erstellung und Pilotierung des Stimulus-Sets (Fragebogenuntersuchung)
- Programmierung und Durchführung der Verhaltens-Pilotstudie
- Programmierung und Durchführung der fMRT-Studie
- Analyse und Verarbeitung der Verhaltens- und fMRT-Daten
- Schreiben der Publikation

Anteil Christian J. Fiebach:

- Projektidee & Konzeption
- Diskussion der Analysemethoden
- Schreiben der Publikation

Anteil Jörg Bahlmann:

- Projektidee
- Schreiben der Publikation

Anteil Jutta L. Mueller:

- Projektidee & Konzeption
- Diskussion der Analysemethoden
- Schreiben der Publikation

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