THE EFFECTS OF NEUROCOGNITIVE AGING ON SENTENCE PROCESSING

DER FAKULTÄT FÜR LEBENSWISSENSCHAFTEN
DER UNIVERSITÄT LEIPZIG
EINGEREICHTE

DISSERTATION

zur Erlangung des akademischen Grades

doctor rerum naturalium,
Dr. rer. nat.

vorgelegt von
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geboren am 04.03.1988 in Berlin

Leipzig, den 18.04.2019
verteidigt am 08.10.2019

Acknowledgments

The time of the PhD has been a fantastic journey in which I grew scientifically and personally. I could have not done this without the help, support and encouragement of my incredible mentors, colleagues, friends, and family. At first, I would like to thank my supervisors and mentors. I am grateful to Angela D. Friederici for the chance to thrive in an environment as nourishing as the MPI, for her guidance and support throughout my PhD time. I would also like to express my sincere gratitude to Lars Meyer who was there at every step of the way and always made time when I needed advice. I am grateful that Lars encouraged me to chair a symposium, supervise a MA thesis project, teach at the University of Leipzig, etc. which all prepared me well to continue my scientific career. I feel also very fortunate that I got the chance to work with Markus Werkle-Bergner on my third study. I have learned a great deal about aging research from him and would like to thank him for all his support. That being said, this collaboration would have not even been possible without Ulman Lindenberger who I would like to thank for this opportunity.

On top of these wonderful mentors and advisors, the work presented in this thesis was supported by many other people at the Max Planck Institute of Human Cognitive and Brain Sciences. I am particularly grateful for the assistance given by Cornelia Henschel, Heike Boethel, Kristiane Klein, Johanna Tegtmeyer and Marie-Theres Götze with the data collection. I would like to thank Fernando Ardente for his help with the stimulus construction. I would like to thank Maren Grigutsch and Burkhard Maess for their methodological advice. I would like to thank Kerstin Flake, Andrea Gast-Sandman and Heike Schmidt Duderstedt from the graphics department for help with posters and figures. However, the PhD time is not only a scientific journey per se but also one where you learn to handle (paper) rejections, to never take reviewer 2 personal and to deal with frustration. Hence, a good network of friends and colleagues is important on top of all the scientific support. Therefore, I would like to thank: Ulrike Kuhl, Clara Ekerdt, Clara Kühn, Nestor Zaragoza, Sandra Martin, Cornelia van Scherpenberg.

BIBLIOGRAPHIC DETAILS

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The Effects of Neurocognitive Aging on Sentence Processing

Fakultät für Lebenswissenschaften, Universität Leipzig

Dissertation

195 Pages, 481 References, 13 Tables, 13 Figures

Across the lifespan, successful language comprehension is crucial for continued participation in everyday life. The success of language comprehension relies on the intact functioning of both language-specific processes as well as domain-general cognitive processes that support language comprehension in general. This two-sided nature of successful language comprehension may contribute to the two diverging observations in healthy aging: the preservation and the decline of language comprehension on both the cognitive and the neural level. To date, our understanding of these two competing facets is incomplete and unclear. While greater language experience comes with increasing age, most domain-general cognitive functions, like verbal working memory, decline in healthy aging. The here presented thesis shows that when the electrophysiological network relevant for verbal working memory is already compromised at rest, language comprehension declines in older adults. Moreover, it could be shown that, as verbal working memory capacity declines with age, resources may become insufficient to successfully encode language-specific information into memory, yielding language comprehension difficulties in old age. Age differences in the electrophysiological dynamics underlying sentence encoding indicate that the encoding of detailed information may increasingly be inhibited throughout the lifespan, possibly to avoid overloading the verbal working memory. However, limitations in verbal working memory could be attenuated by the use of language-specific constraints. That is, semantic and syntactic constraints can be used to establish relations between words which reduces the memory load from individual word information to information about word group. Here, it was found that older adults do not benefit from the use of syntactic constraints as much as younger adults while the benefit of using semantic constraints was comparable across age. Overall, the here presented thesis suggests that previous findings on language comprehension in healthy aging are not contradictory but rather converge on a simultaneous combination of selective preservation and decline of various language-specific processes, burdened by domain-general neurocognitive aging.

Contents

Preface

Across the lifespan, successful language comprehension is crucial for continued participation in everyday life. While older adults do have, in principle, greater experience and expertise with language, healthy aging affects language comprehension in a complex combination of language decline and language preservation. To date, our understanding of these two competing facets is incomplete and unclear. For language decline, previous studies showed that when language processing becomes verbal working memory (vWM) demanding, age-related comprehension difficulties emerge. For language preservation, previous studies showed that older adults have no comprehension difficulties when language processing is not vWM-demanding. This calls the domain-specificity of age-related comprehension difficulties into question. Moreover, comprehension difficulties have been related to brain changes, both on the structural and functional level; however, evidence for this is scarce (see Chapter 1; General Introduction). Therefore, in this thesis, my overarching goal is to contribute to our understanding of the effects of both language-specific and domain-general aging on vWM-demanding sentence comprehension using the electroencephalogram (EEG) . The results of the here presented work gives novel insights into the multifaceted nature of sentence processing including both declines and preservation in healthy aging.

In three studies, the effects of neurocognitive aging on sentence processing were addressed, assessing both language-specific and domain-general cognitive abilities. First, age differences in the electrophysiological basis of sentence processing were investigated in the brain at rest, that is, without the immediate performance of an experimental task (see Chapter 2; Beese, Meyer, Vassileiou, & Friederici, 2017). After the EEG recording at rest, both language-specific and domain-general cognitive abilities were assessed. The results revealed that the language-specific electrophysiological network remained largely intact while progressive changes to an electrophysiological network that is associated with vWM functioning yielded age-related sentence comprehension difficulties. Considering that vWM plays a key role in sentence comprehension, comprehension difficulties may specifically arise when the capacity to encode sentences into vWM declines in old age (see Chapter 3; Beese, Vassileiou, Friederici, & Meyer, submitted). This is because successful encoding of sentences is a prerequisite for accurate sentence comprehension. To this end, the EEG was recorded while participants listened to sentences that they needed to encode and remember for a subsequent comprehension task. The results suggested that sentence encoding in older adults is compromised as reflected by an alteration of the electrophysiological dynamics. While the results of both studies (Beese et al., 2017; Beese et al., submitted) suggest domain-general neurocognitive aging to play a key role in sentence processing, it remained an open question whether older adults would benefit from the use of language-specific constraints to establish relations between words, thereby compressing information and reducing vWM costs. Therefore, in the next study, it was examined whether older and younger adults differ in the extent to which they exploit semantic and syntactic constraints (see Chapter 4; Beese, Werkle-Bergner, Lindenberger, Friederici, & Meyer, 2019). The results indicated that older adults do not benefit from the use of syntactic constraints as much as younger adults, while the benefit of using semantic constraints was similar across age groups. This relative importance of semantic information may suggest a shift in focus from syntactic to semantic information during sentence processing in healthy aging. However, this shift in focus was not affected by vWM limitations in old age.

Overall, the findings of these three studies (Beese et al., 2017; Beese et al., submitted; Beese et al., 2019) make two important contributions to the field of neurocognitive aging of language processing: First, language comprehension is affected by domain-general neurocognitive aging. Second, when disentangling distinct language-specific processes, it becomes clear that language comprehension in healthy aging is affected by differential language-specific declines. Together, this shows that age-related comprehension difficulties are associated with both language-specific and domain-general neurocognitive aging (see Chapter 5; General Discussion).

Chapter 1

General Introduction

1.1 Outline

The framework of neurocognitive aging proposed here illustrates the connections between the subtopics relevant for this thesis: *Cognitive, Structural and Functional Brain Aging* (Figure 1.1).

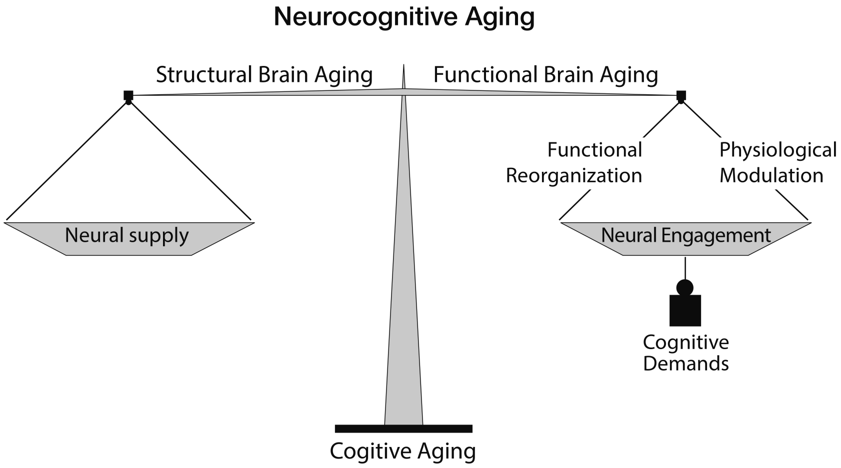

Figure 1.1: Framework of Neurocognitive Aging.

This framework has been synthesized from the prior literature and can be applied to sentence comprehension in healthy aging. This framework postulates that *Cognitive Aging* (see the foot of Figure 1.1) is related to both *Structural* (left side of the scale in Figure 1.1) and *Functional Brain Aging* (right side of the scale in Figure 1.1). First, *Cognitive Aging* of language-specific processes will be discussed, demonstrating that semantic processes are preserved in old age, while syntactic processes decline in particular when sentences are vWM-demanding (Chapter 1.2.2). On this basis, the effects of domain-general cognitive aging on sentence processing will be considered, focusing on vWM. Moreover, sentence comprehension difficulties may relate to both *Structural* and *Functional Brain Aging* (Chapter 1.3). In this context, *Structural Brain Aging* is characterized by the decrease of available neural resources for sentence processing (*Neural Supply*). In contrast, *Functional Brain Aging* is characterized by the *Neural Engagement*, marked by *Functional Reorganizations* of brain regions engaged in sentence processing, on the one side. On the other side, *Functional Brain Aging* is marked by a modulation of the (electro-) physiological network dynamics that support sentence processing (*Physiological Modulation*; Chapter 1.4). That is, both the electrophysiological basis of sentence processing at rest and the electrophysiological correlates of semantic and syntactic processes are altered across the age trajectory. Moreover, healthy aging also affects the electrophysiological correlates of domain-general cognitive functions that support sentence processing. The latter possibly relates to sentence comprehension difficulties with increasing vWM-demands (see *Cognitive Demands* in Figure 1.1). Together, knowing which, to what extent and how brain regions are engaged during sentence processing across the lifespan, sets the stage for discussing the effects of neurocognitive aging on sentence processing. This introduction provides a basic overview for the understanding of the subsequent studies in Chapter 2 (Beese et al., 2017), Chapter 3 (Beese et al., submitted) and Chapter 4 (Beese et al., 2019). The findings of these studies serve as the basis to refine the tentative framework (Figure 1.1) in the General Discussion (see Chapter 5).

1.2 Cognitive Aging

Healthy aging affects sentence comprehension in a complex combination of language preservation and decline (for review, see Shafto & Tyler, 2014). Simple and short sentences are not vWM-demanding and are easily understood by older adults (e.g., Gilchrist, Cowan, & Naveh-Benjamin, 2008; Wingfield, Poon, Lombardi, & Lowe, 1985). In contrast, age-related comprehension difficulties emerge when sentence processing becomes more vWM-demanding, for instance, when sentences are long, ambiguous, or complex (e.g., Feier & Gerstman, 1980; Kemper, 1987; Obler, Fein, Nicholas, & Albert, 1991, respectively). The processing of vWM-demanding sentences has been shown to involve both language-specific and domain-general cognitive processes (e.g., Campbell & Tyler, 2018; Fedorenko, 2014; Wingfield & Grossman, 2006). On this basis, Wingfield and Grossman (2006) synthesized a two-component model that suggests that age-related sentence comprehension difficulties are associated with declines in domain-general cognitive processes while language-specific processes remain preserved. However, this model is neither specific with respect to the exact language processes that may remain preserved nor with respect to the exact domain-general processes that support language comprehension. The findings of this thesis further specify the two-component model by adding multifaceted layers of language-specific and domain-general cognitive functions that contribute to the effects of neurocognitive aging on language processing. Therefore, in the following section, selective and differential age differences in both language-specific (i.e., syntactic and/or semantic) and domain-general (i.e., non-language-specific) cognitive processes will be discussed (for a review, see Diaz, Rizio, & Zhuang, 2016).

1.2.1 Language-Specific Cognitive Aging

Language-specific processes have been found to be differentially affected by healthy aging (e.g., Friederici, Schriefers, & Lindenberger, 1998; Poulisse, Wheeldon, & Segaert, in press; Stine-Morrow, Loveless, & Soederberg, 1996). That is, the processing of the meaning of words and their relations (i.e., semantic processing) has been shown to remain preserved in old age, while the processing of syntactic categories (e.g., nouns, verbs) and their relations (i.e., syntactic processing) has been found compromised in old age (e.g., Friederici et al., 1998). When semantic and syntactic relations between words are established, information becomes compressed which reduces vWM costs (e.g., Bonhage, Meyer, Gruber, Friederici, & Mueller, 2017; Epstein, 1962). It remains an open question whether older and younger adults also differentially exploit semantic and syntactic constraints to reduce vWM demands during sentence processing. Therefore, in Beese et al. (2019), the effects of healthy aging on the use of syntactic versus semantic constraints were investigated (see Chapter 4).

Considering the preservation of semantic processing, on the one side, successful sentence comprehension involves the integration of incoming verbal information into sentence-level representations based on semantic relations. For example, a semantic relation between the words "*wooden*" and "*boat*" may be established by compressing the semantic information of both words into one enriched semantic representation of "*boat*", that is "*wooden boat*" (e.g., Schell, Zaccarella, & Friederici, 2017). When words are embedded in sentences and such semantic relations can be established, the semantics of the sentence facilitates older adults' word recognition either to the same extent (e.g., Balota, Watson, Duchek, & Ferraro, 1999; Bowles & Poon, 1985; Burke, White, & Diaz, 1987; Burke & Yee, 1984; Howard, 1983; Howard, McAndrews, & Lasaga, 1981; Lazzara, Yonelinas, & Ober, 2002; Madden, 1986, 1989; Madden, Pierce, & Allen, 1993; Tree & Hirsh, 2003), or to a greater extent than it does for younger adults (e.g., Balota & Duchek, 1988; Bowles & Poon, 1988; Laver & Burke, 1993; Myerson, Ferraro, Hale, & Lima, 1992). Hence, older adults typically report no comprehension difficulties when reading novels or newspapers (e.g., Light & Burke, 1993) which may also be related to their larger vocabulary (e.g., Brysbaert, Stevens, Mandera, & Keuleers, 2016; Park et al., 2002; Verhaeghen, 2003) and world knowledge relative to younger adults (e.g., Ackerman & Rolfhus, 1999; Beier & Ackerman, 2001). Moreover, neither accuracy nor speed of semantic processing appear to differ between younger and older adults (e.g., Burke et al., 1987; Gunter, Jackson, & Mulder, 1998; Laver, 2009). Overall, these findings indicate that semantic processing remains preserved in old age (for review, see Burke & Shafto, 2008; Wingfield & Stine-Morrow, 2000).

Considering the decline of syntactic processing, on the other side, successful sentence comprehension also requires the integration of incoming verbal information into sentence-level representations based on syntactic relations. For instance, a syntactic relation between the article *"the"* and the noun *"boat"* can be established by compressing the syntactic information of both words into one joint syntactic representation, that is the noun phrase *"the boat"* (e.g., Bonhage et al., 2017; Meyer, Henry, Gaston, Schmuck, & Friederici, 2017; Schell et al., 2017). Previous studies found that older adults engage less in enriched and detailed syntactic processing (e.g., Radvansky, Curiel, Zwaan, & Copeland, 2001; Stine-Morrow et al., 1996). Specifically, both error rates and processing time increase for older relative to younger adults, specifically when vWM-demands are high, that is, for example, when sentences are long, ambiguous, or syntactically complex (e.g., Kemper, 1986; Kemper, Crow, & Kemtes, 2004; Obler et al., 1991, respectively). In the case of long sentences, an increased sentence length has been found to decrease older adults' sentence comprehension accuracy (e.g., Kemper, 1986, 1987; Wingfield et al., 1985). For instance, poorer repetition accuracy was found for 8-word sentences compared to 5-word sentences in older but not in younger adults (Wingfield et al., 1985). Moreover, older adults have also been shown to allocate extra processing time to the point of disambiguation, possibly indicating increased vWM cost due to reanalysis efforts (e.g., Kemper et al., 2004; Kemper & Kemtes, 2002). Other studies have focused on syntactic complexity, which is determined by the deviation of the syntactic structure from the canonical word order (in English, subject-verb-object). Older adults make more comprehension errors and also allocate more time than younger adults to non-canonical (i.e., complex) object relative sentences (object-subject-verb) compared to canonical (i.e., simple) subject relative sentences (subject-verb-object; e.g., Emery, 1985; Feier & Gerstman, 1980; Kemper, 1986, 1987; Norman, Kemper, Kynette, Cheung, & Anagnopoulos, 1991; Obler et al., 1991). This has been related to limited vWM resources in old age (e.g., Just & Carpenter, 1992). Therefore, another line of research attributes age differences in syntactic processing to vWM limitations in old age, that is domain-general cognitive aging (e.g., Caplan & Waters, 1999; DeCaro, Peelle, Grossman, & Wingfield, 2016; Wingfield & Grossman, 2006).

1.2.2 Domain-General Cognitive Aging

Research into cognitive aging has demonstrated that many domain-general cognitive functions, that support sentence processing (e.g., Fedorenko, 2014), decline with age (e.g., Hedden & Gabrieli, 2004). Specifically, a decline in vWM capacity has been suggested to constrain sentence processing in healthy aging (e.g., Caplan & Waters, 1999; DeCaro et al., 2016; Just & Carpenter, 1992; Wingfield & Grossman, 2006). The role of vWM for sentence processing is threefold: 1) the individual vWM capacity constrains sentence processing (e.g., high versus low span readers; Daneman & Carpenter, 1980), 2) sentence materials can tax vWM capacity (e.g., object versus subject relative sentences; Gibson, 1998, 2000, or e.g., long versus short sentences; Carpenter, Miyake, and Just, 1994; Just and Carpenter, 1992), and 3) the task design can tax vWM capacity (e.g., online versus offline tasks; Waters & Caplan, 2001). First, limitations in the individual vWM capacity have been found to increase older adults' error rates and time to process sentences (e.g., Just & Carpenter, 1992; Kemper et al., 2004; Kemtes & Kemper, 1997; Norman, Kemper, & Kynette, 1992; Norman et al., 1991; Radvansky, Gerard, Zacks, & Hasher, 1990). Second, age-related sentence comprehension difficulties have been associated with vWM-demanding sentence materials, in particular sentences that are syntactically complex, ambiguous or long (as discussed in Chapter 1.2.1). Third, vWM resources may also be taxed by the nature of the task assessing sentence comprehension. In post-stimulus, offline tasks, the task probes after the sentence has been fully processed. Therefore, syntactic and semantic information have to be maintained in vWM until the task probes. This increases vWM demands. In comparison, tasks that tap into real-time, online sentence processing such as self-paced reading or listening tasks minimize vWM costs (e.g., Waters & Caplan, 2001). Due to these lower task demands in online tasks, age differences have been suggested to disappear with online compared to offline tasks (e.g., DeDe & Flax, 2016; Waters & Caplan, 2001). Overall, insufficient vWM capacity, vWM-demanding sentence materials and vWM-demanding task designs, all contribute to some extent to age-related sentence comprehension difficulties.

1.3 Neural Aging

The neural basis of age differences in sentence processing is still largely unknown. However, first indications point to an association between age-related sentence comprehension difficulties and both structural and functional brain aging (for review, see Antonenko et al., 2013; Davis, Zhuang, Wright, & Tyler, 2014; Rosselli, Ardila, Matute, & Velez-Uribe, 2014).

1.3.1 Structural Brain Aging

Empirical evidence suggests that age-related sentence comprehension difficulties may be also based on structural brain aging (for review, see Rosselli et al., 2014), in particular on gray matter (e.g., Davis et al., 2014; Tyler et al., 2010) and white matter aging (e.g., Antonenko et al., 2013). Gray matter aging is characterized by region-specific volume reductions and cortical thinning (e.g., Fjell et al., 2014; Raz et al., 2005; Raz, Rodrigue, Head, Kennedy, & Acker, 2004; Salat et al., 2004). On the overall brain level, gray matter aging follows a linear course from early adulthood onwards (e.g., Bartzokis et al., 2001; Fjell et al., 2014; Ge et al., 2002; Walhovd et al., 2005), but the rate varies across brain regions (e.g., Raz et al., 2005; Raz et al., 2004). Regions that mature early in life (e.g., primary sensory cortices) retain relative stability until very late in life (e.g., Kennedy & Raz, 2015; Raz et al., 2005; Raz & Rodrigue, 2006; Raz, Williamson, Gunning-Dixon, Head, & Acker, 2000; Resnick, Pham, Kraut, Zonderman, & Davatzikos, 2003), whereas regions that mature later (e.g., association cortices) are also the first ones to deteriorate (last-in-first-out hypothesis Raz, 2005; Sowell et al., 2003). Within the association cortices, the largest loss and steepest decline was found within the lateral prefrontal cortex (PFC; Raz et al., 2004; Tisserand et al., 2002), which is known to be crucially involved in sentence processing (e.g., Friederici, 2011, 2017). Gray matter aging in the left prefrontal cortex has been associated with an upregulation of contralateral, right prefrontal activity supporting sentence processing in old age (e.g., Tyler et al., 2010).

Moreover, white matter aging has also been shown to contribute to age-related sentence comprehension difficulties. It is marked by the degradation of the myelin sheath around white matter fibers. The extent of this degradation may determine the deceleration of information transfer via the affected fibers (e.g., Jones, Knosche, & Turner, 2013; Wake, Lee, & Fields, 2011), possibly also compromising sentence processing. White matter aging follows a non-linear course, with prolonged white matter maturation throughout adolescence until midlife and subsequent declines (e.g., Bartzokis et al., 2001; Bartzokis et al., 2003; Bartzokis et al., 2004; Courchesne et al., 2000; Ge et al., 2002; Jernigan et al., 2001; Jernigan & Fennema-Notestine, 2004; Lebel et al., 2012; Raz et al., 2005; Raz et al., 2004; Salat, Kaye, & Janowsky, 1999; Sowell et al., 2003; Walhovd et al., 2005). White matter declines are selective and differential: while myelinated primary motor and sensory regions are resilient to white matter aging until very late in life, association fibers are already affected after midlife (e.g., Bender, Volkle, & Raz, 2016; Kochunov et al., 2012). Association fibers relevant for language processing decline even more selectively and differentially (e.g., Yang et al., 2014): association fibers relevant for syntactic processing (i.e., the arcuate fasciculus and the superior longitudinal fasciculus; Brauer, Anwander, Perani, & Friederici, 2013; Skeide, Brauer, & Friederici, 2016; Wilson et al., 2011) decline before association fibers relevant for semantic processing (i.e., the uncinate fasciculus; for an overview on the structural basis of language processing, see Friederici, 2011, 2017). This may underlie both age-related preservation of semantic processing and age-related decline in syntactic processing (Chapter 1.2.1). Importantly, successful sentence comprehension was found to be associated with the uncinate fasciculus in older adults as opposed to the superior longitudinal fasciculus in younger adults (e.g., Antonenko et al., 2013). This suggests some degree of compensation for decreasing structural brain resources available for syntactic processing with advancing adult age.

1.3.2 Functional Brain Aging

Structural brain aging in regions relevant for sentence processing may be accompanied by functional reorganizations of the networks supporting sentence processing, including both language-specific and domain-general regions (e.g., Wingfield & Grossman, 2006). Previous studies showed that older adults engage the same core left-hemispheric perisylvian language network during language processing as younger adults (e.g., Grossman, Cooke, DeVita, Alsop, et al., 2002; Peelle, Troiani, Wingfield, & Grossman, 2010; Tyler et al., 2010; Wingfield & Grossman, 2006). In younger adults, the core left perisylvian functional language network is composed of the left inferior frontal gyrus (IFG), the left superior temporal gyrus/sulcus (STG/S), the left middle temporal gyrus (MTG), the left inferior temporal gyrus/sulcus (ITG/S), the left premotor cortex (PM), and regions within the left inferior parietal lobule (IPL; e.g., Friederici, 2011, 2017; Hagoort & Indefrey, 2014; Hickok & Poeppel, 2007; Price, 2010; Tyler & Marslen-Wilson, 2008). Thereby, semantic processes recruit left S/MTG and IFG (BA 45/47). In comparison, syntactic processes recruit the left IFG (BA 44) and posterior STG, when sentences are resource-demanding, whereas basic syntactic computations recruit the frontal operculum and left anterior STG (e.g., Friederici, 2011, 2017). In addition to those regions recruited by younger adults, older adults also recruit domain-general regions outside the language network (e.g., Peelle et al., 2010; Tyler et al., 2010; Wingfield & Grossman, 2006). From these prior findings, Wingfield and Grossman (2006) synthesized a two-component model that suggests that the functional integrity of the language network remains preserved, while the functional integrity of a domain-general network that supports sentence processing in older adults is compromised. Hence, according to this model, age-related comprehension difficulties are associated with a functional reorganization of the neural networks that are relevant for language processing but that are not language-specific.

More recently, other forms of functional reorganizations have been associated with sentence processing in old age, serving as mechanisms to reach good levels of performance. Specifically, three different mechanisms of functional reorganization have been associated with sentence processing in old age: compensation (Cabeza, 2002), dedifferentiation (Baltes & Lindenberger, 1997), and a hybrid model of compensation and dedifferentiation (compensation-related utilization of neural circuits hypothesis Reuter-Lorenz & Cappell, 2008). A compensatory functional reorganization implies an additional recruitment of neural resources to sustain cognitive performance in one of three ways (Cabeza, 2002; Cabeza et al., 2018; Cabeza & Dennis, 2012). First, in the context of sentence processing, older adults may up-regulate the recruitment of language-specific regions that are also recruited by younger adults like the prefrontal cortex to sustain a good level of sentence comprehension (e.g., Campbell et al., 2016; Grossman, Cooke, DeVita, Alsop, et al., 2002; Peelle, 2019). Second, older adults may upregulate the recruitment of vWM regions (i.e., domain-general regions) on top of the recruitment of language-specific regions (see the two-component model by Grossman, Cooke, DeVita, Alsop, et al., 2002; Rizio & Diaz, 2016; Wingfield & Grossman, 2006). Third, older adults may upregulate the recruitment of regions that are not usually related to sentence processing. For instance, an age-related preservation of sentence comprehension was found associated with an up-regulation of the right hemisphere homologue of the left hemisphere language network (e.g., Meunier, Stamatakis, & Tyler, 2014; Tyler et al., 2010). In each of those three cases, older adults invested more resources than younger adults to achieve similar levels of performance. Altogether these findings show that compensatory recruitment of additional neural resources can preserve accurate sentence comprehension in old age.

However, when performance cannot be sustained in old age (e.g., Peelle et al., 2010), a functional reorganization of neural resources cannot be considered compensatory anymore but reflects merely different neural activation patterns across the age trajectory (i.e., neural dedifferentiation Baltes & Lindenberger, 1997; Ghisletta & Lindenberger, 2003). Accordingly, when sentence comprehension is affected by age, older adults down-regulate language-specific regions (i.e., left IFG) while up-regulating additional, mainly right hemisphere, brain regions outside the core left-lateralized language network, like the right IFG; bilateral superior and/or middle frontal gyrus, right temporal pole, bilateral precentral gyrus (e.g., Davis et al., 2014; Erb & Obleser, 2013; Grossman, Cooke, DeVita, Chen, et al., 2002; Peelle et al., 2010; Tremblay, Dick, & Small, 2013). The down-regulation may indicate a decrease in the ability to use language-specific functions, while the up-regulation may then indicate a limited ability to coordinate brain activity across regions (e.g., Andrews-Hanna et al., 2007).

Decisive for the form of functional reorganization (compensation or dedifferentiation) may be the processing difficulty. For instance, when sentence processing difficulty is low, an up-regulation of brain regions corresponds to maintained sentence comprehension in older adults, contrary to when sentence processing difficulty is high and the up-regulation does not yield maintained sentence comprehension (e.g., Grossman, Cooke, DeVita, Chen, et al., 2002). Generalizing this example in terms of the compensation-related utilization of neural circuits hypothesis (CRUNCH, Reuter-Lorenz & Cappell, 2008): When task difficulty is low, increased brain activity sustains behavioral performance in older adults, supporting the theory of compensation. In contrast, when task difficulty is high, brain activity reaches a plateau or even declines while behavioral performance decreases, supporting the theory of dedifferentiation. However empirical evidence for CRUNCH in sentence processing is scarce. Overall, functional brain aging is characterized by the functional reorganization of the neural networks relevant for language processing (e.g., Crosson, Garcia, McGregor, Wierenga, & Meinzer, 2013; Diaz et al., 2016; Peelle, 2019). However, functional brain aging is not only marked by the functional reorganization of networks but also by the modulation of the underlying (electro-) physiological dynamics of those networks.

1.4 Electrophysiological Aging

Effects of healthy aging on both structural and functional networks relevant for sentence processing may be accompanied by age-related modulations to both the electrophysiological basis at rest (1.4.1) and the electrophysiological correlates of language-specific (1.4.2) and language-relevant but domain-general processes (1.4.3). However, to date, age-related modulations of the electrophysiological underpinnings of sentence processing remain poorly understood. The findings from both Beese et al. (2017, Chapter 2) and Beese et al. (submitted, Chapter 3) contribute to fill this gap.

1.4.1 Electrophysiological Basis At Rest

As modulations of the electrophysiological signal at rest compromise children's sentence processing (e.g., Papagiannopoulou & Lagopoulos, 2016), this may also apply to older adults. Specifically, it is known from animal research that age-related alterations affect the electrophysiological signal (e.g., Barnes, Rao, Foster, & McNaughton, 1992; Luebke, Chang, Moore, & Rosene, 2004; Potier, Rascol, Jazat, Lamour, & Dutar, 1992). At rest, the electrophysiological signal is neither time- nor phase-locked to some extrinsic event and can be characterized by its amplitude, frequency and phase (e.g., Luck, 2005). The quasi-rhythmic, frequency-specific electrophysiological signal may be denoted as oscillatory activity, including delta ($\sim$ 2–4 Hz), theta ($\sim$ 4–8 Hz), alpha ($\sim$ 8–12 Hz), and beta oscillations ($>$ 12 Hz). At its maximum, frequency-specific oscillatory activity or oscillatory power constitutes its peak frequency. For instance, within the alpha frequency band, oscillatory power typically peaks at 10 Hz in younger adults (e.g., Klimesch, 1999). In humans, common age-related alterations of the resting-state EEG signal are threefold: 1) the individual alpha peak frequency (IAF) slows down, 2) oscillatory power across the frequency spectrum decreases, and 3) the functional connectivity between electrodes becomes weaker (e.g., Celesia, 1986; Dustman, Shearer, & Emmerson, 1993; Marsh & Thompson, 1977; Obrist, 1954, 1976; Obrist et al., 1963; Prinz, Dustman, & Emmerson, 1990; Shearer, Emmerson, & Dustman, 1989). There is particularly strong consensus with respect to (1), the IAF slowing with increasing adult age (see Table 1.1; e.g., Aurlien et al., 2004; Chiang, Rennie, Robinson, van Albada, & Kerr, 2011; Klimesch, 1999; Köpruner, Pfurtscheller, & Auer, 1984; Markand, 1990): the IAF declines from approximately 10–10.5 Hz in younger adults to 9–9.5 Hz in older adults ($\sim$70 years of age). The IAF drops even further to 8.5–9 Hz beyond 80 years of age.

With respect to the reductions in oscillatory power during healthy aging (2), findings are differential for specific frequency ranges (Table 1.2). Slower frequency ranges including delta, theta and alpha bands show pronounced power decreases while higher frequency ranges including the beta band show power increases (e.g., Barry & De Blasio, 2017; Dustman, Shearer, & Emmerson, 1999).

Evidence for the weakening of functional connectivity between electrodes (3) is scarce but consistently shows reduced connectivity within the alpha range. However, connectivity within the delta, theta and beta range has paradoxically been shown to either decrease or

Table 1.1: A comprehensive, though not exhaustive, list of well-known studies explicitly reporting alpha peak differences across the lifespan.

	Young Adults		Older Adults	
Study	Peak (Hz)	Age (years)	Peak (Hz)	Age (years)
Babiloni et al. (2006)	10.30	18–50	9.50	51–85
Barry and De Blasio (2017)	9.68	19–26	9.18	60–75
Duffy et al. (1984) *	9.79	30–40	9.03	70–80
Mundy-Castle et al. (1954)	10.32	22	9.39	75
Obrist (1976)	10.20–10.5	< 20	9.0-9.7	60–69
Oken and Kaye (1992) *	9.60	20–29	8.80	90–99
Scally et al. (2018)	10.04	20	8.78	70
Woodruff and Kramer (1979)	10.3	19–25	9	65-88

NOTE: Where age is presented by a single number, it represents the mean age, otherwise the age range.

* Please note that there were more than two age groups; only the youngest and oldest groups are report here.

increase across the lifespan (e.g., Duffy, McAnulty, & Albert, 1996; Kikuchi, Wada, Koshino, Nanbu, & Hashimoto, 2000; Scally, Burke, Bunce, & Delvenne, 2018; Vecchio et al., 2013; Vysata et al., 2014).

Table 1.2: A comprehensive, though not exhaustive, list of well-known studies explicitly reporting electrophysiological alterations of oscillatory power within the delta, theta, alpha, and beta frequency ranges across the lifespan

	Delta		Theta		Alpha		Beta	
Study	Pattern	Range (Hz)	Pattern	Range (Hz)	Pattern	Range (Hz)	Pattern	Range (Hz)
Babiloni et al. (2006)	↓	2–4	–	4–8	↓	8–13	–	13.5–20
Barry et al. (2014)	↓	/	↓	/	↓	/	↑	/
Barry and De Blasio (2017)	↓	0.5–3.5	↓	4–7.5	↓	8–13	↑	13.5–24
Breslau et al. (1989)	↓	0.8–4.3	↓	4.7–7.8	↓	8.2–12.9	↓	13.3–19.9
Duffy et al. (1984)	↓	0–3.75	↓	4–4.75	↓	8–11.75	↑	12–31.5
Duffy et al. (1993)	↓	0.5–3.5	↓	4–7.5	↓	8–11.5	↑	12–31.5
Dustman et al. (1999)	↓	1–4	↓	4–8	↓	8–13	↑	13–30
Polich (1997)	↓	0.25 – 4	↓	4–8	↓	7.5–9.5	–	12–20
Reichert et al. (2016)	↓	0.1–4	↓	4–8	↓	8–10	↑	12–35
Vysata et al. (2012)	↓	0.5–3.5	↓	4–7.5	↓	8–12.5	↑	13–29.5

* Note: ↓ age-related decrease; ↑ age-related increase; – same level between younger and older adults

Such oscillatory alterations across the lifespan appear to also bear functional relevance, as they have been associated with general cognitive functioning (e.g., Grunwald et al., 2001; Grunwald, Hensel, Wolf, Weiss, & Gertz, 2007). For instance, decreased resting-state theta power relates to both better memory performance in younger adults (e.g., Heister et al., 2013; Reichert, Kober, Witte, Neuper, & Wood, 2016; Roca-Stappung et al., 2012) and better language abilities in children (e.g., Papagiannopoulou & Lagopoulos, 2016). Therefore, lower theta power at rest indicates better cognitive functioning on a subsequent task.

To date, there is a critical gap in our understanding of the role of spontaneous intrinsic oscillatory activity at rest for the functional integrity of the language network, how this resting-state network changes across the lifespan, and how this affects language processing. To fill this gap, in Beese et al. (2017), age differences in resting-state theta power were related to sentence comprehension difficulties in old age (see Chapter 2). The results of this study revealed that the language-specific electrophysiological theta network remained intact across the lifespan, while sentence comprehension difficulties in old age were associated with an age-related degradation of the electrophysiological theta network relevant for vWM functioning. Hence, two distinct resting-state theta networks support successful sentence processing across the age trajectory, one related to vWM, and one related to sentence processing. Yet, the engagement of both language-specific and domain-general networks in sentence processing remains to be investigated across the age trajectory.

1.4.2 Language-Specific Electrophysiological Correlates

To date, little is known about lifespan changes to the language-specific electrophysiological correlates of sentence processing. Those studies that are available have focused on the electrophysiological signal that is time-locked (e.g., to the sentence onset or a specific word within the sentence) and phase-locked, constituting event-related potentials (ERP). ERPs related to language-specific processes were found to be lower in amplitude and longer in latency in older compared to younger adults (e.g., Federmeier, McLennan, De Ochoa, & Kutas, 2002; Gunter, Jackson, & Mulder, 1992; Gunter, Vos, & Friederici, 2002; Kutas & Iragui, 1998; Wlotko, Federmeier, & Kutas, 2012). That is the case for semantic processing as indexed by a negative-going waveform over bilateral posterior scalp locations, 300–500 ms after the onset of the event, peaking at 400 ms—the so-called N400 (e.g., Chwilla, Kolk, & Vissers, 2007; Kutas & Hillyard, 1980, 1984; Van Berkum, Brown, Zwitserlood, Kooijman, & Hagoort, 2005; Van Berkum, Hagoort, & Brown, 1999). Specifically, this N400 response was found to be lower in amplitude and delayed in latency in older relative to younger adults, for example, when encountering semantically unexpected words at the end of a sentence (e.g., Federmeier & Kutas, 2005; Federmeier, Van Petten, Schwartz, & Kutas, 2003; Gunter et al., 1992, 1998; Gunter et al., 2002; Harbin, Marsh, & Harvey, 1984; Kutas & Iragui, 1998). This finding may suggest that older adults' efficiency to pre-activate upcoming semantic information as sentences unfold is reduced compared to younger adults (e.g., Federmeier & Kutas, 2005; Federmeier, Kutas, & Schul, 2010; Federmeier et al., 2002). Above and beyond semantic processing, age-related alternations to the electrophysiological correlates of syntactic processing have also been observed. However, those alternations are more selective and differential: While ERPs related to early syntactic processing have been shown age-invariant, those related to later syntactic processes were found to be compromised (e.g., Gunter et al., 2002). Early syntactic processing, like automatic phrase structure building, has been found to be age-resilient. That is, for instance, younger and older adults show similar electrophysiological responses to phrase structure violations (e.g., Gunter et al., 2002), namely an early left anterior negativity (ELAN) over frontal sites, 100–300 ms after the stimulus onset, peaking at 200 ms (e.g., Friederici, 1995; Hahne & Friederici, 1999). In contrast, slightly later syntactic processes, like the processing of morpho-syntactic information, was found to be affected by healthy aging. That is, in response to gender agreement violations (e.g., Alatorre-Cruz et al., 2018), older adults show lower amplitudes in the left anterior negativity (LAN) over frontal sites, 300–500ms after the stimulus onset (e.g., Friederici, Hahne, & Mecklinger, 1996). Such age differences also pertain to even later syntactic processes (e.g., Alatorre-Cruz et al., 2018; Gunter et al., 2002) that are indexed by a positive deflection over centro-parietal sites, 400–800 ms after the stimulus onset, peaking at 600 ms—the so-called P600 (e.g., Fiebach, Schlesewsky, & Friederici, 2001; Hagoort, Brown, & Groothusen, 1993; Kaan, Harris, Gibson, & Holcomb, 2000; Osterhout & Holcomb, 1992). For instance, when recovering from difficulties processing severe phrase structure violations (e.g., Gunter et al., 2002) or gender agreement violations (e.g., Alatorre-Cruz et al., 2018), older adults show a smaller and delayed P600. However, when syntactic processing difficulty is low, for instance, when participants have to recover from grammatical number violations (e.g., Kemmer, Coulson, De Ochoa, & Kutas, 2004), no such age differences appear. These findings suggest that older adults differ from younger adults in the recovery from higher but not lower syntactic processing difficulties (e.g., Alatorre-Cruz et al., 2018). Altogether, these studies show that language-specific electrophysiological correlates of sentence processing are selectively and differentially affected by healthy aging (e.g., Federmeier et al., 2002; Gunter et al., 1992; Gunter et al., 2002; Kutas & Iragui, 1998; Wlotko et al., 2012).

In contrast to those ERP findings, nothing is known about lifespan changes in the oscillatory responses to sentence processing (i.e., the signal that is time-locked but not phase-locked to the event) that have been observed in younger adults (e.g., Bastiaansen and Hagoort, 2015; Ding, Melloni, Zhang, Tian, and Poeppel, 2016; for review, see Meyer, 2017). In younger adults, semantic processing has been related to decreased beta power (e.g., Bastiaansen, van der Linden, Ter Keurs, Dijkstra, & Hagoort, 2005; Lewis & Bastiaansen, 2015; Lewis, Schoffelen, Schriefers, & Bastiaansen, 2016; Wang et al., 2012), elicited by, for example, semantically unexpected words at the end of the sentence (e.g., Wang et al., 2012). In addition, syntactic processes have also been associated with oscillatory dynamics in younger adults, specifically with theta band oscillations (e.g., Bastiaansen, Magyari, & Hagoort, 2010; Bastiaansen, van Berkum, & Hagoort, 2002a; Weiss et al., 2005). For instance, variations in syntactic complexity (e.g., Weiss et al., 2005), the detection of syntactic violations (e.g., Bastiaansen, van Berkum, & Hagoort, 2002b) and the general unfolding of sentences (e.g., Bastiaansen et al., 2010; Bastiaansen et al., 2002a) have been related to increased theta power. It was suggested that increased theta power relates to syntactic integration processes (e.g., Bastiaansen et al., 2010; Bastiaansen et al., 2002a). Yet, nothing is known about lifespan changes of such oscillatory dynamics is response to semantic and syntactic processes. To address this gap, alterations of the oscillatory dynamics in response to sentence processing were examined in Chapter 3, Beese et al. (submitted). However, interestingly, the results revealed that age-related sentence comprehension difficulties may associate with alterations to the electrophysiological correlates of domain-general not language-specific processes that support sentence processing.

1.4.3 Domain-General Electrophysiological Correlates

Age-related declines in domain-general cognitive functions that crucially constrain sentence processing (e.g., Fedorenko, 2014) may alter language-specific electrophysiological correlates of sentence processing, yielding age-related sentence comprehension difficulties. More specifically, sentence comprehension relies on sufficient vWM capacity to successfully encode syntactic and semantic information as sentences unfold (e.g., Just & Carpenter, 1992). The individual vWM capacity has been found to alter the electrophysiological correlates of sentence processing in younger adults (e.g., Fiebach et al., 2001, 2002; Vos, Gunter, Kolk, & Mulder, 2001). That is, language-specific ERPs (specifically, LAN and P600) were more widely distributed and enlarged in amplitude when vWM capacity was low as compared to when it was high. Considering that vWM capacity decreases across the lifespan (e.g., Bopp & Verhaeghen, 2005), differences between older and younger adults may resemble differences between individuals with low and high vWM capacity, respectively. Following this proposal, language-specific electrophysiological correlates of sentence processing may be altered by the age-related decline in vWM capacity. Substantiating this hypothesis, when taking vWM capacity into account, older adults with low vWM capacity exhibit even more delayed ERPs (specifically the N400; Federmeier & Kutas, 2005; Federmeier et al., 2003). Altogether these findings suggest that vWM capacity modulates the electrophysiological correlates of sentence processing in younger and older adults; but it is possible that vWM capacity may play an even more important role.

When vWM capacity declines across the lifespan, it may become insufficient for the successful encoding of sentences into vWM. Hence, age-related sentence comprehension difficulties may also be associated with an inefficient encoding of sentences (Friedman & Johnson Jr., 2014), possibly reflected by altered electrophysiological correlates of encoding. The encoding of sentences may be successful when syntactic and semantic information are transformed into memory traces (e.g., Wagner et al., 1998) through temporarily synchronous neural activity (i.e., simultaneous, frequency-specific neuronal firing; Buzsaki & Draguhn, 2004; Engel & Singer, 2001; Tallon-Baudry & Bertrand, 1999). Encoding success can be measured by subtracting the encoding-related neural activity of later not remembered (LNR) items from that of later remembered (LR) items, yielding the subsequent memory effect (SME, originally coined "difference in subsequent memory" by Paller, Kutas, and Mayes (1987)). Greater positive amplitudes were found for LR than LNR information between 400 and 800 ms after the stimulus onset over frontal and parietal sites (e.g., Fabiani & Donchin, 1995; Fabiani, Karis, & Donchin, 1986; Karis, Fabiani, & Donchin, 1984; Neville, Kutas, Chesney, & Schmidt, 1986; Paller et al., 1987; Paller & Wagner, 2002; Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980). Moreover, encoding success has been associated with increases in oscillatory activity within the theta band range (e.g., Buzsaki, 1996; Fell & Axmacher, 2011; Klimesch, 1996; Klimesch, Doppelmayr, Schimke, & Ripper, 1997; Lisman & Idiart, 1995; Raghavachari et al., 2001; Staudigl & Hanslmayr, 2013). Theta oscillations have been suggested to play a role in both organizing multiple items (e.g., Axmacher et al., 2010; Lisman & Idiart, 1995) and binding items to context information (e.g., Staudigl & Hanslmayr, 2013; Tort, Komorowski, Manns, Kopell, & Eichenbaum, 2009), two abilities that appear relevant for establishing semantic and syntactic relations between words as sentences unfold. When the amplitude or power is greater for LR than LNR information, this is called a positive SME, otherwise it is a negative SME (e.g., Otten & Rugg, 2001;

Paller & Wagner, 2002). While positive SMEs rely on task-specific networks, recruiting more left-hemispheric frontal regions (e.g., PFC) for verbal material (e.g., Henson, Rugg, Shallice, Josephs, & Dolan, 1999) and right-hemispheric posterior sites (e.g., posterior parietal cortex, hippocampal formation) for pictorial material (e.g., Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998), negative SMEs have been shown to recruit the default-mode network (i.e., anterior and posterior midline cortex, the temporo-parietal junction, and the medial prefrontal cortex, as suggested by Daselaar, Prince, and Cabeza, 2004; Park and Rugg, 2008; Raichle et al., 2001; Shrager, Kirwan, and Squire, 2008; for a meta-analysis, see Kim, 2011). Age effects may be more differential in negative than positive SMEs (for a review, see Maillet & Rajah, 2014). That is, while positive SMEs differ little, if at all, as a function of age, negative SMEs have more consistently been reported attenuated or reversed with age (e.g., de Chastelaine, Mattson, Wang, Donley, & Rugg, 2015, 2016; Friedman & Trott, 2000; Koen, Horne, Hauck, & Rugg, 2018; Mattson, Wang, de Chastelaine, & Rugg, 2014). Age differences in negative SMEs may thus affect the encoding efficiency of older adults (e.g., Friedman & Johnson Jr., 2014; Friedman, Nessler, & Johnson Jr, 2007). Generally, age-related encoding deficits (e.g., Cansino, Trejo-Morales, & Hernandez-Ramos, 2010; Grady et al., 1995) were found to be reflected by attenuated frontal positive SMEs in older than in younger adults (e.g., Kamp & Zimmer, 2015; Kuo, Liu, Ting, & Chan, 2014; Morcom, Good, Frackowiak, & Rugg, 2003). However, contrary to those studies, others found no age-related SME differences (e.g., Gutchess, Ieuji, & Federmeier, 2007; Shing, Brehmer, Heekeren, Bäckman, & Lindenberger, 2016; Tellez-Alanis & Cansino, 2004): here, both younger and older adults exhibit larger activity over fronto-central regions for LR compared to LNR items.

It remains an open question whether encoding efficiency in older adults contributes to age-related difficulties in sentence comprehension. Therefore, in Beese et al. (submitted), the specific role of sentence encoding for successful sentence comprehension was examined across the age trajectory (Chapter 3). Age-related alterations of the electrophysiological correlates of vWM encoding were hypothesized to compromise sentence comprehension in old age. The results suggest that limited vWM capacity necessitated older adults to inhibit the encoding of information that would otherwise have overloaded their vWM capacity. This may also imply that older adults do not extract detailed information in a bottom-up way as younger adults but rather extract the gist of information in a top-down way. These findings suggest that sentence comprehension is affected in old age by an alteration of the electrophysiological correlates of domain-general higher cognitive functions that support sentence processing.

Such alterations of the electrophysiological dynamics should be related to structural brain aging in the future, as sentence comprehension difficulties have been suggested to relate to both functional and structural brain aging (see the tentative framework in Figure 1.1, in Chapter 1.1).

1.5 Research Questions

In summary, the present thesis aims at understanding the effects of both language-specific and domain-general neurocognitive aging on language comprehension using the EEG. In contribution to this aim, three major research questions were addressed:

(1) Is sentence comprehension compromised in healthy aging by age-related alterations of the language-specific and/or domain-general electrophysiological network dynamics at rest (see Chapter 2; Beese et al., 2017)?

(2) Are age-related sentence comprehension difficulties associated with age-related alterations of the electrophysiological correlates of sentence encoding (see Chapter 3; Beese et al., submitted)?

(3) Do older and younger adults differ in the extent to which they benefit from semantic and syntactic constraints to reduce vWM costs (see Chapter 4; Beese et al., 2019)?

The answers to these questions contribute to our incomplete and unclear understanding of the complex combination of complementary language decline and language preservation.

Chapter 2

Study 1

Temporally and spatially distinct theta oscillations dissociate a language-specific from a domain-general processing mechanism across the age trajectory[1]

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Published in Scientific Reports in 2017

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[1] This chapter is adapted from the article published in Scientific Reports by Beese et al. (2017)

Abstract

The cognitive functionality of neural oscillations is still highly debated, as different functions have been associated with identical frequency ranges. Theta band oscillations, for instance, were proposed to underlie both language comprehension and domain-general cognitive abilities. Here we show that the ageing brain can provide an answer to the open question whether it is one and the same theta oscillation underlying those functions, thereby resolving a long-standing paradox. While better cognitive functioning is predicted by low theta power in the brain at rest, resting state (RS) theta power declines with age, but sentence comprehension deteriorates in old age. We resolve this paradox showing that sentence comprehension declines due to changes in RS theta power within domain-general brain networks known to support successful sentence comprehension, while low RS theta power within the left-hemispheric dorso-frontal language network predicts intact sentence comprehension. The two RS theta networks were also found to functionally decouple relative to their independent internal coupling. Thus, both temporally and spatially distinct RS theta oscillations dissociate a language-specific from a domain-general processing mechanism.

2.1 Introduction

Language comprehension in general remains remarkably stable across the lifespan; sentence comprehension, however, is known to decline with age (e.g., Caplan, Dede, Waters, Michaud, & Tripodis, 2011; Friederici, Schriefers, & Lindenberger, 1998). This age-related decline holds particularly for working memory-intensive sentences (e.g., Just & Carpenter, 1992), which predominantly tax the encoding and retention of verbal information across increased intervals (e.g., Gibson, 2000; Just & Carpenter, 1992; Lewis, Vasishth, & Van Dyke, 2006; Meyer, Grigutsch, Schmuck, Gaston, & Friederici, 2015).

The ability to encode working memory-intensive sentences, such as structurally complex, ambiguous, or long sentences (e.g., Friederici, Steinhauer, Mecklinger, & Meyer, 1998; King & Just, 1991; Vos, Gunter, Kolk, & Mulder, 2001), is a major determinant of language comprehension. That is, language comprehension requires the encoding and retention of verbal information over either increased hierarchical or sequential distances while simultaneously processing intervening verbal material, potentially interfering with already encoded information. Therefore, the encoding success can be affected quantitatively by the number of words (i.e., capacity-based, Just & Carpenter, 1992) as well as qualitatively by the memory strength (i.e., decay-, interference- and structure-based, Gordon, Hendrick, & Johnson, 2001; Mecklinger, Schriefers, Steinhauer, & Friederici, 1995; Tan, Martin, & Van Dyke, 2017; Van Dyke & McElree, 2006). On complex sentences, readers with a high memory span perform faster and more accurately than low-span readers (e.g., Friederici, Schriefers, & Lindenberger, 1998; King & Just, 1991; Mecklinger et al., 1995; Vos et al., 2001). This difference is supported by electrophysiological studies showing that event-related brain potentials (ERPs) associated with sentence processing difficulty (e.g., Kaan, Harris, Gibson, & Holcomb, 2000) increase for low-span as compared to high-span readers (e.g., Vos et al., 2001). Likewise, processing differences have been found during the disambiguation of ambiguous sentences, with larger ERP differences for high-span readers than for low-span readers (e.g., Friederici, Steinhauer, et al., 1998). Such differences are particularly pronounced when ambiguities are extended (e.g., Friederici, Steinhauer, et al., 1998), possibly suggesting (e.g., Just & Carpenter, 1992) that low-span readers' verbal working memory resources are exhausted by the increased duration of an ambiguity (e.g., Gibson, 2000; Lewis et al., 2006; McElree, Foraker, & Dyer, 2003; Vos et al., 2001).

Given its critical role for sentence comprehension, the decline of verbal working memory capacity with age (e.g., Dobbs & Rule, 1989) could also underlie the decline in sentence comprehension in the elderly (e.g., Salthouse, 1994). When sentence processing is working memory-intensive, older adults perform worse than young adults. Syntactically complex sentences are processed slower and less accurately by older as compared to young adults (e.g., Caplan et al., 2011; Kemper, 1986, 1987; Obler, Fein, Nicholas, & Albert, 1991; Stine-Morrow, Ryan, & Leonard, 2000; Wingfield & Grossman, 2006). Likewise, older adults comprehend ambiguous sentences less accurately than young adults, behaving much like low-span readers across age groups (e.g., Kemper, Crow, & Kemtes, 2004). Finally, increasing sentence duration also decreases older adults' sentence comprehension accuracy (e.g., Kemper, 1986, 1987; Wingfield, Poon, Lombardi, & Lowe, 1985): Poorer repetition accuracy was found for 8-word sentences compared to 5-word sentences in older but not in young adults (Wingfield et al., 1985).

Despite substantial behavioural evidence for the age-related decline in working memory-intensive sentence comprehension, its neural underpinnings as measured by electrophysiological methods remain highly controversial. In healthy young adults, event-related theta power changes have not only been linked to verbal working memory in general (e.g., Karrasch, Laine, Rapinoja, & Krause, 2004; Klimesch, 1999) but also specifically to the verbal working memory demands during sentence comprehension (e.g., Bastiaansen, van Berkum, & Hagoort, 2002a; Meyer et al., 2015). That means theta power seems to be modulated both by domain-general as well as domain-specific working memory demands. For example, during general verbal working memory tasks increased theta power has been found to predict better performance. In comparison, during sentence comprehension, increased theta power has been found for more compared to less complex sentences (e.g., Weiss et al., 2005) showing that the theta rhythm may be modulated by memory-taxing sentences (e.g., Bastiaansen, van Berkum, & Hagoort, 2002b), too. The increase in theta power may be linked to increased synchronisation within the functional network of working memory (e.g., Bastiaansen et al., 2002b). In contrast to those event-related studies mentioned afore, in the resting state (RS), decreases in theta power seem to predict better verbal working memory (e.g., Garrett, Kovacevic, McIntosh, & Grady, 2010; Heister et al., 2013; Reichert, Kober, Witte, Neuper, & Wood, 2016; Roca-Stappung et al., 2012). This may imply that, in the brain at rest, less specificity and more variability in frequency-specific neural synchrony may predict optimal functioning at task. This may be due to better readiness for settling into a new state during task-related processing. This is in line with proposals from previous studies (e.g., Garrett, Kovacevic, McIntosh, & Grady, 2013). In sum, that means, there is a critical gap in our understanding of the role of spontaneous neural activity, recorded in the brain at rest, particularly for the functional integrity of the language network. Our study is a first attempt to bridge this gap linking changes in RS theta power to working memory-intensive sentence comprehension.

Given the association between RS theta power and verbal working memory, and given the association between verbal working memory and sentence comprehension across the lifespan, RS theta power could be a plausible lifespan predictor of working memory-intensive sentence comprehension. This hypothesis, however, faces a paradox in the light of three findings (Figure 2.1): (a) while RS theta power decreases across the lifespan (e.g., Vlahou, Thurm, Kolassa, & Schlee, 2014), (b) and low theta power in the RS indicates good verbal working memory, verbal working memory and sentence comprehension do not improve with age (c1) but instead deteriorate in older adults (c2). Hence, the association between RS theta power, verbal working memory, and sentence comprehension appears to change across the lifespan.

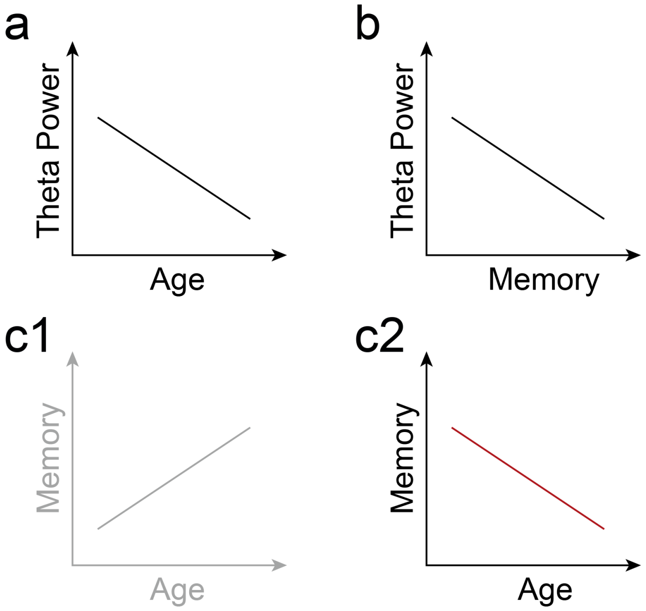

Figure 2.1: Schematic overview of paradox as a consequence of two coinciding patterns: (a) an age-related decrease in resting-state theta power and (b) lower resting-state theta power predicting good working memory performance. Taking (a) and (b) together, one would predict (c1), an age-related increase in working memory. However, previous studies found (c2) working memory decreases with age.

Here we resolve this paradox, extending previous findings (e.g., Heister et al., 2013): First, we established RS theta as the electrophysiological marker of working memory-intensive sentence comprehension across three age groups (young, middle-aged and older adults). To this end, we correlated RS theta power across the age trajectory with performance on a working memory-intensive sentence comprehension task. Second, we associated age-related decreases in RS theta power to domain-general cognitive abilities supporting sentence comprehension. This approach enabled us to assess the functional integrity of the brain networks underlying working memory-intensive sentence comprehension. Our findings established a crucial role of RS theta power for successful sentence comprehension that is preserved across the lifespan in spite of an age-related cognitive decline.

2.2 Methods

2.2.1 Participants

Data from 57 healthy right-handed (Oldfield, 1971) participants divided into three equally-sized age groups (young: 9 male; mean age: 25 years; *SD*: 1 year; middle-aged: 9 male; mean age: 43 years; *SD*: 2 years; older: 8 male; mean age: 65; *SD*: 3 years) were analysed. The age ranges of the three groups were restricted to approximately one decade each (i.e., 22–28, 40–48 and 61–70 years of age) to assure comparable variance of age across groups. Participants were native speakers of German, had normal or corrected-to-normal vision, and did not suffer from neurological disorders or hearing loss (hearing threshold $\leq$ 25dB as assessed by standard audiometry, Oscilla SM910-B, Aarhus, Denmark)[2]. Participants were tested for cognitive impairment (Mini-Mental State Examination 2, Folstein, Folstein, White, & Messer, 2010), assuring that no participant suffered from dementia. Education was matched across age groups ($\geq$ 14 years of education). All participants gave written informed consent prior to any testing. The study was approved by the ethics committee of the University of Leipzig. The experiment was conducted according to the approved guidelines.

2.2.2 Neuropsychological Measures

On the first day of testing, all participants underwent a cognitive screening to ensure healthy ageing. The screening included measures of working memory (digit span forward and backward (Aster, Neubauer, & Horn, 2006), non-word repetition task (Welte, 1981), and Counting Span (Case, Kurland, & Goldberg, 1982)), verbal intelligence (similarities task and vocabulary task), non-verbal intelligence (matrices and block tasks; Aster et al., 2006), and auditory attention (Auditory Flankers; Chan, Merrifield, and Spence, 2005)[3].

2.2.3 Stimuli

The experimental items for the working memory-intensive sentence comprehension task were 128 encoding sentences, each consisting of two conjoined clauses containing one subject and

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[2] For more information on the audiometric assessment, see the Supplements

[3] For more information on the neuropsychological tests, see the Supplements

two direct objects each (see Table 2.1). Subjects and objects were all animate in order to avoid associated processing differences (Bonin, Gelin, & Bugaiska, 2014). Additionally, subjects and objects differed in grammatical gender within clause, which later served as a retrieval cue. The gender of subjects and objects was counterbalanced across the stimulus set. Subjects and objects were matched for word length (i.e., number of syllables) and word frequency class within and across sentences (Goldhahn, Eckart, & Quasthoff, 2012). This minimised processing differences due to both word length (Spoehr & Smith, 1973) as well as word frequency (Allen, Badecker, & Osterhout, 2003). Furthermore, this ensured similar encoding demands for each word, which are affected by both syllable count (Luo, Husain, Horwitz, & Poeppel, 2005) and lexical frequency (Halgren et al., 2002). Subjects' encoding performance was assessed through a combination of a retrieval sentence and a comprehension question. The retrieval sentence operationalised retrieval via two pronouns, one of the subject's and one of the object's gender, thus referring to a unique subject or object within the encoding sentence. In the example retrieval sentence *Die von ihr Angekündigte war nervös* (*The one (she) announced by her was nervous*), the phrase *die von ihr* is pointing to exactly one noun of the encoding sentence. Thereby, *ihr (her)* is pointing to the subject, die Moderatorin (the presenter) who acts upon the female object, *die Künstlerin (the artist)*, referred to by *die (she).* The subsequent comprehension question assessed retrieval success (and thus, indirectly, encoding success of the encoding sentence) by asking either for the correct item *(Was the artist nervous?)*, a gender lure *(Was the actor nervous?)* or a word category lure *(Was the presenter nervous?).* The introduction of lure questions aimed at keeping the amount of correct yes- and no-responses equal. Moreover, the lures necessitated whole sentence processing as category lures emphasised the encoding of both the conjoined clauses whereas gender lures emphasised the encoding of the gender information of all nouns.

Table 2.1: Stimulus materials; encoding sentence with examples of both subject and object retrieval sentences as well as comprehension questions and subsequent feedback.

Phase		Example	
Encoding (5.0–7.8 s, A)		Der Moderator hat den Schriftsteller und die Sängerin angekündigt und die Moderatorin hat den Schauspieler und die Künstlerin angekündigt. *The presenter (m) had announced the writer (m) and the singer (f) and the presenter (f) has announced the actor (m) and the artist (f).*	
		Subject	Object
Retrieval (3.5 s, V)		Die sie Ankündigende war nervös. *The one (f) announcing her was nervous*	Die von ihr Angekündigte war nervös. *The one (f) announced by her was nervous.*
Question (< 4 s, V)	corr	War die Moderatorin nervös? *Was the preseter (f) nervous?*	War die Künstlerin nervös? *Was the artist (f) nervous?*
	gen-l	War die Sängerin nervös? *Was the singer (f) nervous?*	War die Schauspielerin nervös? *Was the actor (f) nervous?*
	cat-l	War die Künstlerin nervös? *Was the artist (f) nervous?*	War die Moderatorin nervös? *Was the presenter (f) nervous?*
Feedback (1.0 s, V)		☺/ ☹	

Note: (f) = female, (m) = male; corr = correct, gen-l = gender lure, cat-l = category-lure; A = Auditory, V = visual

Taking into account the number of clauses (i.e., 2), of objects within clauses (i.e., 2) and of subjects per sentence (i.e., 2), 8 variants of each encoding sentence were created in order to counterbalance the gender information of each noun. Those 8 variants were combined with 4 variants of the retrieval sentence varying in gender information of the 2 determiners ensuring that the retrieved items were half male and half female. Hence there were 32 combinations for each of the 128 experimental items which were distributed via Latin Square across 32 lists. This distribution also accounted for the various retrieval types (subject or object retrieval), the retrieval position within the encoding sentence, as well as question types (correct or lure) across lists (within items) and also within lists (across items). With 19 participants in each age group not all 32 variants of each experimental items could be presented. However, this does not pose a limitation as balancing the factors within each list assured equivalent conditions for each participant.

In addition to the experimental items, 64 filler items were included to avoid habituation effects and the build-up of experimental strategies. In comparison to the experimental items, the encoding sentences of the filler items were syntactically more complex (i.e., object-relative clauses and topicalisations). In order to further maximise the difference to the experimental items where gender information was introduced in form of suffixes (e.g., act- or act-ress), in filler sentences gender information was introduced in form of nouns of biological gender (e.g. uncle - aunt). However, while syntactic differences were maximised, other features like syllable count and word frequency were matched to the experimental items in order to disguise the interests of this study. Furthermore, all content words across experimental and filler stimuli were uniquely used in order to avoid memory consolidation effects, which could have confounded the results. The 64 filler items were added to the 128 experimental items for each of the 32 lists, which were then pseudo-randomised.

2.2.4 Procedure

The experiment was conducted over two days within a period of no more than 7 days. On the first day, participants underwent audiometer testing and cognitive screening (see Neuropsychological Measures). On the second day, we recorded the electroencephalogram (EEG) at rest and then during the working memory-intensive sentence comprehension task. The sentence comprehension task involved an encoding and a retrieval sentence as well as a comprehension question, and feedback to the subject (see Table 2.1), in this order. Auditory stimuli were presented via headphones (Sennheiser, HD202). To ensure the same hearing level for all participants, the volume was adjusted to 38dB above the individual hearing threshold (as determined by the method of limits (Herrmann, Henry, Haegens, & Obleser, 2016) on the day of the experiment before setting up the EEG). Visual stimuli were presented in white font (Arial, size 30) on a grey screen (17 inch, Sony Multiscan E220). An experimental trial started with the auditory presentation of an encoding sentence followed by a jittered pause of 1.0–1.5 seconds. A visual retrieval sentence was then presented, querying either a subject or an object from the preceding stimulus sentence. A jittered pause of 1.5–2.0 seconds followed. A comprehension question followed, asking for the correct answer (CORR) in 50 % of trials, for a gender lure (GEN-L) in 25 % of trials and for a syntactic category lure (CAT-L) in 25 % of trials. The participants had a response time window of 4 seconds to respond with either "yes" or "no" by pressing either of two single-button response boxes placed individually under their left and right index finger. Button assignment was counterbalanced across participants. After the response was given, visual feedback was provided in form of a happy or sad emoticon. A trial ended with a jittered inter-trial interval of between 1.5–2.0 seconds.

2.2.5 Data Acquistion

Resting state EEG from each subject was acquired for 5 minutes with the subject's eyes closed (EC) followed by 5 minutes with the subject's eyes open (EO), with eye opening prompted by a pure tone of 500 Hz presented at 85 dB. EC and EO were both recorded to enable the calculation of subjects' individual theta frequency (see Data Analysis). Therefore, sufficient data length per condition was crucial to compute reliable estimates of the theta power from the resting-state EEG signal. Maltez, Hyllienmark, Nikulin, and Brismar (2004) suggested a minimum length of 2 minutes after data cleaning which requires longer segments to start with. Hence, 5 minutes per condition provided a reliable basis for robust results. Data were acquired within a pass-band from DC to 270 Hz at a sampling rate of 1,000 Hz from 63 electrodes. The setup was referenced against the left mastoid and grounded to the sternum. The vertical and horizontal electro-oculogram (EOG) was acquired with bipolar electrodes below and above the right eye as well as at the outer canthi of both eyes, respectively. The scalp electrodes were placed according to the international 10–20 system in an elastic cap (Electro Cap International, Inc., Eaton, OH, USA) connected to a 72-channel Refa amplifier (TMS International B.V., Odenzaal, The Netherlands). Electrode impedances were kept below 5kΩ.

2.2.6 Data Analysis

All analyses were performed in MATLAB® (The MathWorks, Inc., Natick, MA, USA). EEG data were analysed using the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). First, two differently filtered data sets were generated from the raw RS EEG data (EC and EO)[4]: First, a band-pass filtered data set for statistical analysis (zero-phase two-pass fourth-order 0.5–45 Hz Butterworth filter); second, a high-pass filtered data set (zero-phase finite-impulse-response one-pass 3624th-order 1-Hz Kaiser filter), optimal for independent component analysis (ICA; Winkler, Debener, Muller, & Tangermann, 2015). Both data sets were re-referenced to the average of all electrodes (excluding the EOG) and segmented into 2-second epochs to facilitate artefact detection. Artefact detection was performed on the high-pass-filtered data set, involving a two-step procedure: First, muscle artefacts were detected using a semi-automatic, distribution-based approach ($z > 9$) and rejected after visual inspection (EC: mean rejection rate = 8.55 %, *SD* = 7.36 %; EO: mean rejection rate = 11.22 %, *SD* = 6.97 %), taking into account the waveform morphology. In a second step, the data were low-pass filtered (zero-phase finite impulse response one-pass Kaiser filter) to 150-Hz to eventually down-sample the data to 300 Hz. Thereby, the low-pass filtered frequency corresponds to the Nyquist frequency of the down-sampled data. These steps accelerate the subsequent ICA. 40 independent components (IC) were computed from a larger set of channels which required a dimension reduction via principle component analysis beforehand. Those ICs that reflected heartbeat, eye movements or eye blinks as well as electrode noise were detected based on visual inspection of the components' waveform morphology, power spectrum, and scalp topography[5]. Artefact ICs were removed from the band-pass filtered data (mean number of rejected ICs: 11.70, *SD* = 1.99; same for all age groups, $F(2,56) = 2.26$, $p = 0.11$), which thereafter was used for all further analyses. After removing A1 and A2 due to leftover noise, the data were re-referenced to the average of all remaining electrodes, and the mean potential within trial was subtracted. The data set was then split into EC and EO. The number of RS trials was pseudo-randomly reduced to the common minimum of 90 trials across all participants—first, trials from the first 30 seconds of the recordings were chosen, and then, trials from the remainder of the data were selected randomly. Using a Hann taper, frequency analysis via FFT was then performed in steps of 1 Hz from 1–25 Hz on the EC and EO data. Oscillatory power was log-transformed. Because of substantial inter-individual variance in individual band peak frequencies within

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[4] For more details on filter-optimized data cleaning, see the Supplements

[5] For a detailed description on the visual detection of the ICs, see the Supplements

and across age groups (Köpruner, Pfurtscheller, & Auer, 1984), each subject's individual alpha peak frequency was detected in order to determine the individual frequency range of the theta band (Clark et al., 2004; Wingfield et al., 1985). First, we preselected an extended alpha frequency range (i.e., 7–14 Hz) and electrodes of interest (Pz, P3, P4, P5, P6, P7, P8, P9, P10, POz, PO3, PO4, PO7, PO8, O1, O2, and Oz) separately for the EC and EO data (Grandy et al., 2013)[6]. Second, the EO power spectrum within this range was subtracted from the EC power spectrum. Third, the maximum peak within the difference spectrum was defined as the individual alpha peak frequency (IAF; Lansbergen, Arns, van Dongen-Boomsma, Spronk, & Buitelaar, 2011). IAF was then used as anchor point to constrain the individual theta frequency band into a range from (IAF – 6 Hz) to (IAF – 2 Hz) (adapted from Caso et al., 2012; Klimesch, 1999). Subsequent RS analyses were then performed on the EC data (Finnigan & Robertson, 2011).

The effects were source-localised using a frequency-domain beamformer (dynamic imaging of coherent sources, DICS Gross et al., 2001). In a first step, a volume conductor was made based on a template Boundary Element Method (BEM) head model (Oostenveld, Stegeman, Praamstra, & van Oosterom, 2003). In a second step, this template head model was joined with template sensor positions in accordance to the electrode set up used in this study to create a forward model within a 1-cm-spaced three-dimensional grid that was used for all participants. In a third step, the spatial filter estimated from the cross-spectral density matrix of each subject the power of the sources along every point of the grid, with a signal-to-noise ratio of 3 %. Finally, the Neural Activity Index (Van Veen, van Drongelen, Yuchtman, & Suzuki, 1997) was computed to remove the center-of-head bias[7].

For source-level coherence analysis, three-dimensional time courses of source moments were derived from the single-segment preprocessed EEG data by multiplying the single-segment EEG with the individual spatial filter from the DICS beamforming analysis. The source grid was masked for the significant grid points ($p < .05$, uncorrected), and three-dimensional dipole moments were extracted for each volume-conductor grid point within the language-specific and the domain-general effects, respectively. The time course for each grid point then underwent singular value decomposition, arriving at a single time course per grid point (Gross et al., 2001; Meyer et al., 2015). On these time courses, the same FFT frequency analysis that was used for the sensor-level data was performed, now restricted to the individual theta band. Finally, coherence analysis was performed on the complex Fourier-spectra (Rappelsberger & Petsche, 1988) for all pairs of dipoles within and across

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[6] For more information in the alpha peak detection, see the Supplements

[7] For more information on the source localization, see the Supplements

the two source-level effects. However, as coherence between areas decays with increasing inter-area distance due to volume conduction (Winter, Nunez, Ding, & Srinivasan, 2007), the results may be confounded by larger inter-network and smaller intra-network source distances. For this reason, a supplementary analysis was performed using a blind source separation algorithm within individual. To this end, first, the single-trial source-level time courses from the coherence analysis were downsampled to 100 Hz to speed up later source separation. Second, the time courses were band-pass filtered (finite-impulse-response two-pass 266th-order filter; Parks & McClellan, 1972) to match the individual theta band range. Third, an ICA was used to extract 10 independent components, aiming to show that the grid points of the two separate networks would indeed cluster around two different independent components, indicating their functional dissociation. Fourth, the component patterns were masked for all grid points included in the two networks. For each grid point, we then determined the independent component that was maximally represented at the grid points.

2.2.7 Statistical Analysis

Two performance measures were computed: the percentage of correctly comprehended sentences and d-prime scores. D-prime scores were calculated by subtracting the z-transformed false alarm rate (FA) from the z-transformed hit rate (H) (d-prime = z(H) − z(FA)). FA or H of 0 was corrected by 1/N and FA or H of 1 was corrected by (N-1)/N, with N being the number of trials (Macmillan & Creelman, 2005). Analyses of variance (ANOVAs) regressed age group separately against both performance measures. All further analyses were done on the basis of d-prime, as it provides the more sensitive behavioural measure. D-prime was related to the EEG data to assess the relevance of RS theta power for working memory-intensive sentence comprehension. Analyses of covariance (ANCOVAs) were computed for each electrode with age group as factor and RS theta power as covariate of interest, both predicting d-prime (Eid, Gollwitzer, & Schmitt, 2010). To assess age-related differences in RS theta power, an ANOVA was computed at each electrode with age group as factor predicting theta power. To account for multiple comparisons, the false discovery rate (FDR, Benjamini & Hochberg, 1995) procedure was used to correct p-values across electrodes. Additionally, those age-related differences in RS theta power were related to variations in domain-general cognitive functions. For this purpose, in a first step, the experimental measure, d-prime, was correlated with the performance measures of the cognitive screening. In a second step, ANCOVAs were performed at each electrode regressing age group against RS theta power controlling for those measures significantly related to d-prime (after FDR-correction). Measures dissolving the relation between age group and RS theta power indicate their link to age-related RS theta power differences. Finally, in analogy to the sensor-level data, an ANCOVA was performed, with source power predicting behavioural performance depending on the age group. Similarly, an ANOVA was performed with age group as factor predicting the source power. The anatomical labels for the significant clusters (uncorrected) were determined from the MNI atlas (Mazziotta et al., 2001). For statistical analysis of source-level coherences, a series of paired-samples t-test was performed, separately comparing the mean coherence of dipole moments within each network (i.e., internal coherence of all dipole pairs within the language network, internal coherence of all dipole pairs within the domain-general network) to the mean coherence of dipole moments across the two networks (i.e., coherence between all pairs that included one dipole from each the language network and the domain-general network). In addition, we also compared the internal coherence of the language network to the internal coherence of the domain-general network. This comparison was substantiated by an additional statistical analysis on source separated component data. We first assessed the difference in the distributions of independent components across networks using within-participant Wilcoxon rank sum tests. The single-subject test statistics from these tests were then submitted to group-level analysis using a one-sample Wilcoxon signed-rank test, hypothesising that the two networks cluster around two different components.

2.3 Results

The working memory-intensive sentence comprehension task used in this study assessed encoding success through a combination of a retrieval sentence and a comprehension question (see Table 2.1 and Methods). Behavioural performance was quantified through calculating d-prime scores as well as the percentage of correctly comprehended sentences (Figure 2.2). The ANOVA a showed a main effect of age group, $F(2,54) = 11.74$, $p = 5.86 \times 10^{-5}$, $\eta^2 = 0.30$, indicating that d-prime decreases with age (Figure 2.2a). Similarly, the ANOVA regressing age group against the percentage of correctly comprehended sentences indicated that sentence comprehension declines with age, $F(2,54) = 12.07$, $p = 4.66 \times 10^{-5}$, $\eta^2 = 0.31$ (Figure 2.2b).

In addition to the working memory-intensive sentence comprehension task, a cognitive screening was performed to, on the one side, ensure healthy ageing of our participants and, on the other side, examine domain-general cognitive abilities associated with the working memory-intensive sentence comprehension task. The results showed significant correlations (FDR-corrected) between d-prime and measures of verbal working memory as well as at-

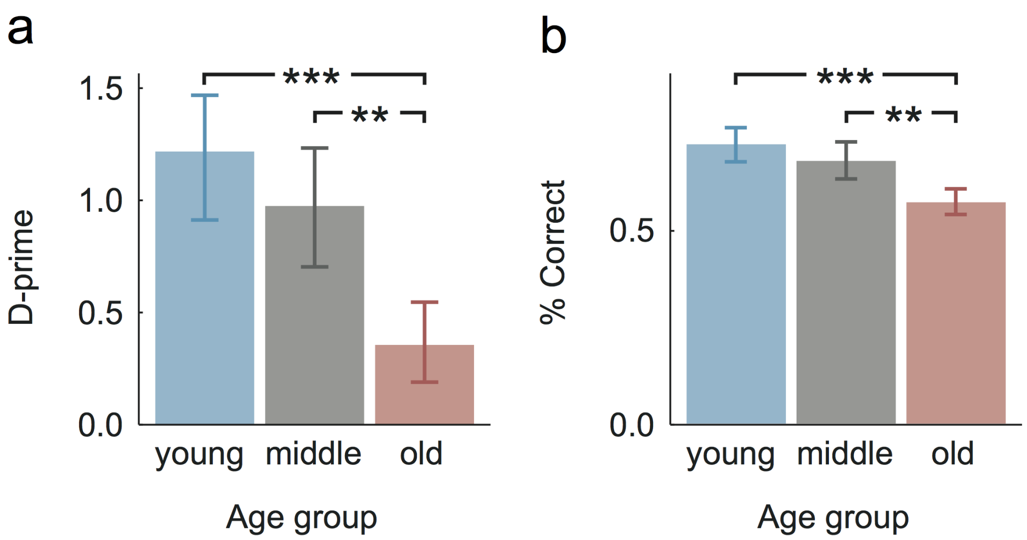

Figure 2.2: Behavioural results: (a) average d-prime scores; (b) average percentage of correctly comprehended sentences; both for the three age groups (25, 43 and 65 years of age, error bars indicate the standard error). For both measures, age groups differed in sentence comprehension performance, such that older subjects showed a reduced sentence comprehension performance relative to young and middle-aged adults (*** = $p < .001$; ** = $p < .01$).

tention (see Methods): the non-word repetition task (r = .45, $p = 5 \times 10^{-4}$), the digit span forward (r = .04, $p = 5 \times 10^{-4}$), the digit span backward (r = .51, $p = 1 \times 10^{-5}$) and the Auditory Flankers Task (r = -.41, $p = 2 \times 10^{-3}$). All of those measures declined with age (non-word repetition: F = .45, $p = 5 \times 10^{-4}$; digit span forward: F = .04, $p = 5 \times 10^{-4}$; digit span backward: F = .51, p = 1×10^{-5}; Auditory Flankers: F = -.41, $p = 2 \times 10^{-3}$; Table 2.2). Given that those domain-general measures are all significantly correlated with the sentence comprehension task, this may suggest a role for the age-related decline in domain-general cognitive abilities in the increased difficulties in working memory-intensive sentence comprehension with age. This proposal is substantiated by our resting state findings.

Table 2.2: Age-related declines in domain-general cognitive abilities; reporting means (standard deviations) as well as the statistical output from the ANOVAs regressing age group against the neuropsychological measures.

Task	Young	Middle	Old	F	p
Digit span task forward	11(2)	11(2)	10(2)	4	.03
Digit span task backward	10(2)	8(2)	6(2)	17	<.001
Non-word repetition task	28(3)	28(3)	25(4)	5	.01
Auditory flankers task	0.01(0.05)	0.05(0.06)	0.10(0.08)	9	<.001

Resting state EEG data from each subject were analysed in the frequency domain using the fast fourier transform (FFT). Statistical analyses were performed hypothesis-driven on the RS data in the theta frequency band. A peak in the theta frequency band could be observed in all three age groups (see Figure 2.3). The presence of such theta peaks justifies to test for the functional relevance of theta oscillations for cognitive abilities.

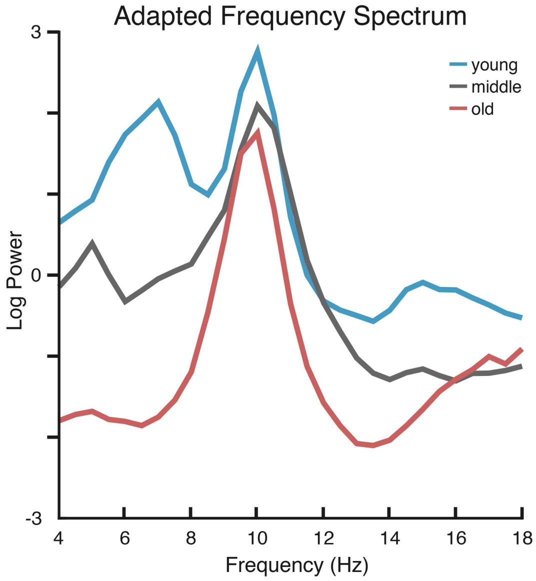

Figure 2.3: Theta peak in the IAF adjusted frequency spectrum (4–18 Hz) of one sample younger, middle-aged and older adult. The theta peak shifts downwards within the typical theta range with advancing adult age while theta power also declines.

To control for effects within neighbouring frequency bands, we also looked at the delta (1–4Hz), alpha (8–12Hz), and beta bands (12–25Hz), none of which showed any additional effects. For source localisation of the theta effect, we used a beamformer in the frequency domain. An analysis of covariance (ANCOVA) on the RS data at each electrode, regressing age group and RS theta power against d-prime, showed main effects of age group at all electrodes (all $F(2{,}51)$ between 12.92 and 19.91, all p between 4.05×10^{-7} and 2.89×10^{-5}, all η^2 between 0.33 and 0.44; false discovery rate (FDR) corrected, and main effects of RS theta power (Figure 2.4a) at electrodes TP9 ($F(1{,}51) = 12.28$, $p = 9.62\times 10^{-4}$, $\eta^2 = 0.19$; FDR-corrected) and P9 ($F(1{,}51) = 13.25$, $p = 6.36 \times 10^{-4}$, $\eta^2 = 0.20$; FDR corrected; Figure 2.4b). There were no interaction effects at any electrode (all $F(2{,}51)$ between 0.80 and 1.68, all p between 0.20 and 0.92) indicating that the relation between theta and d-prime was not affected by any age-related changes. The main effect of RS theta was source localised predominantly to the left-hemispheric dorso-frontal cortex (i.e., at the intersection of the left pre- and postcentral and middle frontal gyrus as well as the pars triangularis) and, less consistently, to the right anterior inferior and middle temporal gyrus (all $F(1{,}51)$ between 4.05 and 11.34, p between 0.002 and 0.05, uncorrected; Table 2.3; (Figure 2.4c).

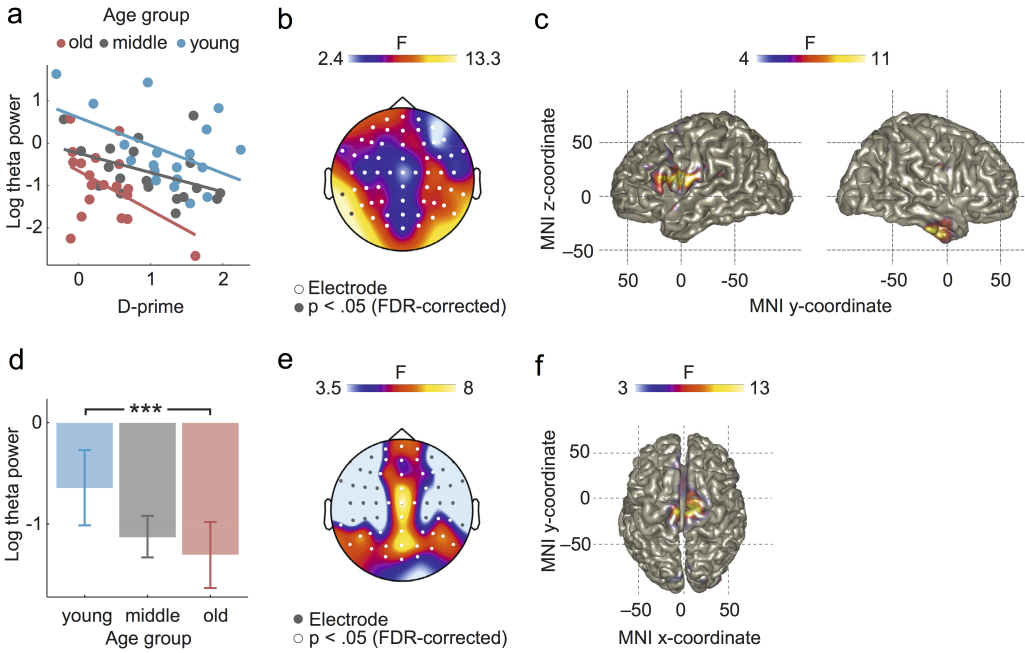

Figure 2.4: Mechanisms supporting sentence comprehension1; **3a-c**: Overview of EEG results supporting language-specific mechanism (ANCOVA on log RS theta power at each electrode, regressing age group and RS theta power against d-prime) (a) scatter plot of log RS theta power at TP9 and P9 predicting sentence comprehension per age group; (b) statistical map of the main effect for RS theta predicting sentence comprehension (F is log-scaled) (c) source-level results of main effect for RS theta power predicting sentence comprehension (F is log-scaled); **3d-f**: Overview of EEG results supporting a domain-general mechanism (ANOVA on age group predicting log RS theta power): (d) average log RS theta power for three age groups (25, 43 and 65 years of age, error bars indicate the standard error). Age groups differed in log RS theta power such that older adults showed reduced log RS theta power relative to young adults (*** = $p < .001$); (e) statistical map of the main effect for age group predicting log RS theta power (F is log-scaled); (f) source-level results of the main effect for age effect group predicting log RS theta power.

The ANOVA at each electrode, regressing age group against RS theta power, showed main effects of age group (Figure 2.4d) at 36 centro-frontal and -posterior electrodes (all $F(2{,}54)$ between 3.76 and 7.92, all p between 9.60×10^{-3} and 0.03, all η^2 between 0.12 and 0.23; Figure 2.4 e), showing that RS theta power decreases with age. This age-related effect was source-localised to bilateral midline regions (i.e., a region shared by bilateral supplementary motor areas, the left superior frontal gyrus and the right mid-cingulum; all $F(2{,}54)$ between 3.17 and 12.65, all p between 3.00×10^{-5} and 0.05, uncorrected; Table 2.3, Figure 2.4f). To assess whether this effect is related to a more specific cognitive function, a post-hoc ANCOVA was performed at each electrode regressing age group against RS theta power controlling for domain-general cognitive abilities earlier shown to support working memory-intensive sentence comprehension. Indeed, we found that the inclusion of the non-word repetition task in the model dissolved the effect of age group on theta (all $F(2{,}51)$

between 0.47 and 7.54, FDR-corrected), indicating its relation to age-related theta decreases over midline regions. All other domain-general cognitive measures that were correlated with the experimental task did not impact the relationship between age group and RS theta power.

Table 2.3: Source-level results ($p < 0.05$, uncorrected) of both the language-specific effect for RS theta power predicting sentence comprehension as well as the domain-general effect for RS theta. Anatomical labels are taken from the Automated-Anatomical-Labelling brain atlas. Cluster peak coordinates are given in Montreal-Neurological-Institute (MNI) space.

Cluster	Region	F-value (peak)	MNI coordinates (mm) X	Y	Z
Language-specific					
Left	postcentral gyrus	11.34	−66	−5	19
	precentral gyrus	10.80	−56	5	19
	pars triangularis	9.55	−46	25	19
	middle frontal gyrus	6.30	−36	5	49
Right	inferior temporal gyrus	9.91	64	−15	−31
	middle temporal gyrus	7.31	54	5	−31
Domain-general					
Left	medial frontal gyrus	7.29	−6	35	49
	supplemental motor areas	9.92	−6	15	59
	superior frontal gyrus	5.86	−16	15	49
Right	supplementary motor areas	12.65	4	−15	69
	medial frontal gyrus	6.09	4	35	39

We reasoned that if the language-specific and the domain-general effect indeed reflect distinct functional networks, subserving distinct cognitive sub-processes of sentence comprehension, the networks should also exhibit a high degree of functional coupling internally, but a significantly lower degree of functional coupling with each other. To follow this post-hoc hypothesis, a source-level coherence analysis on the reconstructed dipole time courses was performed. The results showed that source-level coherence within each of the two networks was higher than coherence across those two networks (internal coherence within the language network: $t(56) = –5.91$, $p = 2.10 \times 10^{-7}$; internal coherence within the domain-general: $t(56) = –4.02$, $p = 1.75\times 10^{-4}$). In other words, the coherence between the language-specific and the domain-general network was lower than the coherence observed separately within the language-specific network and within the domain-general network coherence. In addition, the coherence of sources within the language network did not significantly differ from the coherence of sources within the domain-general network ($t(56) = –1.11$, $p = .27$). An additional source separation procedure showed that this result is not confounded by volume conduction but instead the time courses of the two networks cluster around different independent components ($z = 3.76$, $p = 1.68 \times 10^{-4}$). Together, this strongly supports a functional independence of the two resting state networks (Figure 2.5).

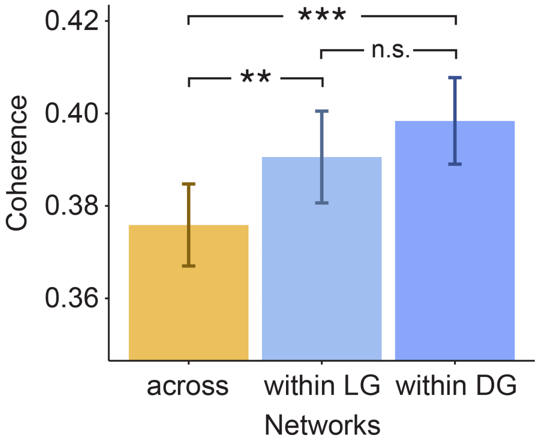

Figure 2.5: Source-level coherence analysis shows that the coherence of sources within the language-specific network and also within the domain-general network is higher than the coherence of sources across those two networks (*** $p < .001$, ** $p < .01$); coherence does not differ significantly across networks1 (n.s. = not significant; error bars indicate the standard error); LG = language, DG = domain-general.

In sum, we found both a performance-related, language-specific and an age-related, domain-general theta effect with distinct scalp topographies and neural generators. While the scalp topographies already hint at different underlying networks, the source localisation allows for a stronger claim that the scalp-level effects were generated by at least partially non-overlapping brain networks and reflect two distinct mechanisms—one specifically underlying sentence comprehension, the other related to an age-related impairment of domain-general cognitive functions supporting sentence comprehension.

2.4 Discussion

This study addresses a long-standing paradox: Prior research found RS theta power to be negatively correlated with verbal working memory abilities, but also to decrease with age. While this would predict performance in working memory-intensive sentence comprehension to increase with age, this is certainly not the case. Our results resolve this paradox, suggesting that RS theta oscillations dissociate two spatially and temporally distinct networks supporting different mechanisms. On the one side, RS theta power over left-hemispheric dorso-frontal and right anterior temporal regions was found to predict sentence comprehension abilities independently of age. On the other side, we found an age-related decline in RS theta power over central recording sites to be associated with verbal working memory. Moreover, such domain-general cognitive abilities supporting sentence comprehension could be functionally decoupled from the language-specific sentence comprehension abilities. Together this suggests that both older and young adults rely on the same core sentence processing mechanism (e.g., Tyler et al., 2010) located within the dorsal perisylvian language network (e.g., Catani, Jones, & ffytche, 2005; Friederici, 2011; Price, 2010)—but that older adults exhibit a performance decline in working memory-intensive sentence comprehension due to changes within the association network subserving domain-general supplementary cognitive functions (e.g., Wingfield & Grossman, 2006).

Across the age trajectory, the results revealed an association between working memory-intensive sentence comprehension and RS theta power generated in regions frequently associated with syntactic processing (e.g., Friederici, 2011; Meyer, Obleser, Kiebel, & Friederici, 2012; Price, 2010; Saur et al., 2008): predominantly left-hemispheric dorso-frontal regions and, to a minor degree, the right anterior temporal lobe. This association is independent of age as no interaction was found between RS theta power and age group to explain the behavioural performance. Therefore, while many other cognitive abilities decline with age (e.g., Dobbs & Rule, 1989), the results of the current study suggest that the core sentence comprehension network stays largely intact along the age trajectory. Possibly, the preservation of this performance-related mechanism throughout the lifespan hints at a compensating role for age-related structural alterations of the language-relevant left-hemispheric dorso-frontal brain regions by functional activation shifts. Previous studies have shown a progressive longitudinal decrease in prefrontal grey and white matter volume across the age trajectory (e.g., Raz et al., 2005), which coincides with functional activation shifts from posterior to anterior brain regions (e.g., Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008). To substantiate this proposal, further investigation of the structural neuroanatomy underlying our theta generators is needed.

While the association between dorso-frontal RS theta power and working memory-intensive sentence comprehension can explain the behavioural results within each age group, it does not explain the substantial age-related decline in working memory-intensive sentence comprehension. Instead, we found an indication of spatially and temporally distinct RS theta oscillations that may instead drive this age-related decline in sentence comprehension performance. This effect is most pronounced over the central electrodes, Fz, Cz, Fpz and Pz, with neural generators predominantly in bilateral frontal to central midline regions. We could relate this age-related RS theta power decrease to variations in general verbal working memory performance, more precisely, to variations in the repetition of non-words of increasing syllable length indicating the capacity of the phonological store. Phonological storage, in turn, has been shown to play a role in working memory-demanding sentence comprehension (e.g., Pettigrew & Hillis, 2014). Therefore, the age-related decline in RS theta power over bilateral frontal to central midline regions associated with working memory differences possibly contributes to the decline in working memory-intensive sentence comprehension. In fact, this is in line with previous findings associating theta over electrode Fz generated by sources along the cingulate as well as the medial frontal cortex with working memory (e.g., Hsieh & Ranganath, 2014; Onton, Delorme, & Makeig, 2005; Scheeringa et al., 2008; Scheeringa et al., 2009). Such frontal midline theta (FMT) was found stronger for high compared to low performers in working memory tasks (e.g., Hsieh, Ekstrom, & Ranganath, 2011). More specifically, FMT has been mainly linked to tasks involving order memory, but not item memory (e.g., Hsieh & Ranganath, 2014). This could explain why the results only showed a link to the non-word repetition task but not to the other working memory tasks included in the cognitive screening (see Methods). The nature of this non-word repetition task involves the memory for the order of phonologically distinctive syllables together constituting individual non-words of increasing length. Hence the order of the syllables is crucial to remember the item. However, generally the link between age-related RS theta power decreases and functional variation in verbal working memory has to be tested more directly by future studies to validate our proposal.

The distinction between the age-related, domain-general and the performance-related, language-specific theta effect can also be observed from their distinct generators. In the mammalian brain, theta-band oscillations can be generated by the hippocampocortical loop—either by the hippocampus itself or by cortical regions within this loop (e.g., Miller, 1991). On the one hand, hippocampal theta, associated with memory formation (e.g., Daselaar et al., 2001), may be related to the age-related decline in RS theta power connected to domain-general functioning. On the other hand, cortical regions within the hippocampocortical loop may underlie the language-specific mechanism observed here. This also implies that the location of a theta generator determines its functionality being either language-specific or domain-general. However, this needs further investigation with the help of spatially fine-grained methodologies. Furthermore, it suggests that future studies should use paradigms which manipulate the stimuli in such a way that language-specific processes can be disentangled from domain-general working memory processes. Such paradigms would ensure the dissociation of different underlying oscillatory networks. This way the field of neuronal oscillations could move forward to categorising frequency bands not only by their function but also by their neural generators.

In sum, this study is the first to identify two spatially as well as temporally distinct theta band oscillations subserving distinct functions during sentence processing. The present results show that RS theta power across left-hemispheric dorso-frontal language regions underlies a language-specific mechanism and hence may serve as robust electrophysiological marker of intact sentence comprehension across the lifespan. Our results, moreover, suggest a dissociable domain-general mechanism associated with a decline of supplementary cognitive functions supporting working memory-intensive sentence comprehension—reflected in decreased RS theta power over bilateral midline regions. In sum, we suggest that working memory-intensive sentence comprehension declines with age due to underlying changes in domain-general brain networks, despite the preservation of the core sentence processing network across the lifespan.

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Chapter 3

Study 2

Age Differences in Encoding-Related Alpha Power Reflect Sentence Comprehension Difficulties[1]

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Submitted to Frontiers in Aging Neuroscience in 2019

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[1] This chapter is adapted from the article submitted to Frontiers in Aging Neuroscience by Beese, Vassileiou, Friederici, and Meyer (submitted)

Abstract

When sentence processing taxes verbal working memory, comprehension difficulties arise. This is specifically the case when processing resources decline with advancing adult age. Such decline likely affects the encoding of sentences into working memory, which constitutes the basis for successful comprehension. To assess age differences in encoding-related electrophysiological activity, we recorded the electroencephalogram from three age groups (24, 43, 65 years). Using an auditory sentence comprehension task, age differences in encoding-related oscillatory power were examined with respect to the accuracy of the given response. That is, the difference in oscillatory power between correctly and incorrectly encoded sentences, yielding subsequent memory effects (SME), was compared across age groups. Across age groups, we observed an age-related SME inversion in the alpha band from a power decrease in younger adults to a power increase in older adults. We suggest that this SME inversion underlies age-related comprehension difficulties. With alpha being commonly linked to inhibitory processes, this shift may reflect a change in the cortical inhibition–disinhibition balance. A cortical disinhibition may imply enriched sentence encoding in younger adults. In contrast, resource limitations in older adults may necessitate an increase in cortical inhibition during sentence encoding to avoid an information overload. Overall, our findings tentatively suggest that age-related comprehension difficulties are associated with alterations to the electrophysiological dynamics subserving general higher cognitive functions.

Keywords: Aging, alpha band, encoding, neural oscillations, sentence comprehension

3.1 Introduction

Sentence comprehension remains generally well preserved across the adult lifespan (Shafto & Tyler, 2014). However, when sentence processing taxes verbal working memory (vWM), comprehension difficulties arise, in particular with advancing adult age (e.g., Feier & Gerstman, 1980; Kemper, 1986; Obler, Fein, Nicholas, & Albert, 1991), that is, when vWM capacity declines (e.g., Bopp & Verhaeghen, 2005). One prerequisite for accurate sentence comprehension is the successful encoding of sentences into vWM as sentences unfold. Age-related comprehension difficulties may reflect an inefficiency in old age to encode sentences into vWM (Friedman & Johnson Jr., 2014). Here, we examined this hypothesis by comparing the neural correlates of sentence encoding, indirectly indicated by comprehension accuracy, across the lifespan.

While substantial behavioral evidence on age differences in vWM-taxing sentence comprehension shows lower accuracy and longer response times in older than younger adults (e.g., Kemper, 1986; Kemper, Crow, & Kemtes, 2004; Obler et al., 1991), there are only few studies on age differences in the electrophysiological correlates of sentence comprehension (e.g., Alatorre-Cruz et al., 2018; Gunter, Vos, & Friederici, 2002). Previously, age differences in both syntactic and semantic processing have been related to altered event-related potentials (ERP). While ERPs related to early syntactic processes have been found age-invariant, those related to later syntactic processes have been shown compromised. For example, under high vWM load, compromised processing of the agreement of syntactic features resulted in a diminished left anterior negativity and P600 in older compared to younger adults (Alatorre-Cruz et al., 2018). But even when sentence material is not specifically vWM-taxing, the P600 is diminished and delayed, for instance, in response to phrase structure violations (Gunter et al., 2002). This may indicate more general syntactic processing difficulties in older adults (e.g., Fiebach, Schlesewsky, & Friederici, 2001; Gibson, 1998; Kaan, Harris, Gibson, & Holcomb, 2000; Osterhout & Holcomb, 1992). Like the P600, the N400 component, which is associated with semantic processing (Kutas & Hillyard, 1980, 1984; Van Berkum, Brown, Zwitserlood, Kooijman, & Hagoort, 2005; Van Berkum, Hagoort, & Brown, 1999), has been shown to be diminished and delayed in older compared to younger adults (e.g., Federmeier, McLennan, De Ochoa, & Kutas, 2002; Gunter, Jackson, & Mulder, 1992; Kutas & Iragui, 1998; Wlotko, Federmeier, & Kutas, 2012). Overall, compared to younger adults, older adults exhibit lower ERP amplitudes and longer latencies during sentence comprehension (Gunter et al., 1992; Kutas and Iragui, 1998; e.g., Federmeier et al., 2002; Friederici et al. 2002 in: Gunter et al., 2002; Wlotko et al., 2012).

While ERP evidence indicates detrimental effects of aging on vWM-taxing sentence comprehension, ERPs are limited to the assessment of evoked (i.e., time– and phase-locked) neural activity. In contrast, here we scrutinized on oscillatory power changes that reflect both evoked and induced electrophysiological dynamics (Pfurtscheller & Lopes da Silva, 1999; Sarnthein, Petsche, Rappelsberger, Shaw, & von Stein, 1998). In general, oscillatory power changes within the theta (4–8 Hz), alpha (8–12 Hz), and beta (15–30 Hz) frequency bands have been related to sentence comprehension (e.g., Bastiaansen and Hagoort, 2015; Ding, Melloni, Zhang, Tian, and Poeppel, 2016; for review see Meyer, 2017). Syntactic processing and specifically syntactic integration of single words into sentences has been related to increased theta-band power (e.g., Bastiaansen, Magyari, & Hagoort, 2009; Bastiaansen, van Berkum, & Hagoort, 2002; Haarmann & Cameron, 2005; Meyer, Grigutsch, Schmuck, Gaston, & Friederici, 2015). In comparison, a decrease in alpha-band power associates with vWM encoding of syntactic information (Bastiaansen et al., 2009; Vassileiou, Meyer, Beese, & Friederici, 2018), while an increase in alpha-band power associates with vWM storage of syntactic information (e.g., Bonhage, Meyer, Gruber, Friederici, & Mueller, 2017; Haarmann & Cameron, 2005; Meyer, Obleser, & Friederici, 2013; Weiss et al., 2005). Finally, a decrease in beta-band power associates with semantic and predictive processing (e.g., Lewis & Bastiaansen, 2015; Wang et al., 2012; Weiss & Rappelsberger, 1996). Yet, the hypothesis that age-related sentence comprehension difficulties may be reflected by changes to oscillatory dynamics has not been pursued thus far.

We hypothesized here that age-related sentence comprehension difficulties may arise from a sentence encoding inefficiency at old age (Friedman & Johnson Jr., 2014). Therefore, in the current study, we investigated age differences in the oscillatory dynamics underlying sentence encoding. The quantification of oscillatory activity during successful encoding was based on encoding behavior. Specifically, we compared the difference in oscillatory power between later correctly comprehended, or later-remembered (LR), sentences, and later incorrectly comprehended, or later-not-remembered (LNR), sentences. This difference constitutes the subsequent memory effect (SME; Paller, Kutas, & Mayes, 1987; Paller & Wagner, 2002). SMEs reflect oscillatory dynamics that index the accessibility of the information that needs to be encoded for accurate sentence comprehension. SME paradigms are thus well suited to investigate a possible link between age-related sentence comprehension difficulties and sentence encoding inefficiency. Prior literature from memory research describes positive SMEs (i.e., encoding-related oscillatory power of LR $>$ LNR) in the theta band (e.g., Friese et al., 2013; Karrasch, Laine, Rapinoja, & Krause, 2004; Osipova et al., 2006) and negative

SMEs (i.e., encoding-related oscillatory power of LR $<$ LNR) in the alpha and beta bands in younger adults (e.g., Hanslmayr & Staudigl, 2014; Otten, Henson, & Rugg, 2001; Schott, Richardson-Klavehn, Heinze, & Duzel, 2002). The effects of healthy aging on SMEs are controversial, including age-invariant SMEs (e.g., Shing et al., 2010), SMEs only in younger but not in older adults (Friedman, Ritter, & Snodgrass, 1996; Friedman & Trott, 2000; Kamp & Zimmer, 2015), and attenuated and even inverted SMEs in older compared to younger adults (de Chastelaine, Mattson, Wang, Donley, & Rugg, 2015; Maillet & Rajah, 2014; Mattson, Wang, de Chastelaine, & Rugg, 2014). However, none of these studies probed the encoding of entire sentences. It remains an open question whether age-related differences in encoding-related oscillatory neural activity associate with age-related sentence comprehension difficulties.

We hypothesized that age differences in successful sentence encoding are reflected by specific age differences in the encoding-related oscillatory power. To this end, we compared the oscillatory power of correctly and incorrectly encoded sentences, as indicated by sentence comprehension accuracy, between younger, middle-aged, and older adults. As previous studies showed encoding inefficiency already around midlife (Cansino, Trejo-Morales, & Hernandez-Ramos, 2010) but comprehension difficulties only after midlife (Sommers, 2015), it was crucial to include the group of middle-aged adults. We expected vWM limitations in older adults to associate with attenuated or even inverted SMEs compared to younger adults. Specifically, we hypothesized to find a positive theta-band SME (Klimesch, 1999) and negative alpha– and beta-band SMEs (Hanslmayr & Staudigl, 2014) in younger adults. Our results confirmed that the negative alpha-band SME in younger adults is attenuated in middle-aged adults and inverted in older adults. This may indicate a decreased encoding efficiency associated with age-related sentence comprehension difficulties.

3.2 Methods

3.2.1 Participants

An original sample of 59 healthy right-handed native speakers of German, divided into three age groups (20 younger, 19 middle-aged and 20 older adults), participated in this study. After excluding below-chance performers (see Statistical analysis), data from 18 younger adults (8 male; mean age = 24.39 years; SD = 1.30 years), 16 middle-aged adults (8 male; mean age = 42.50 years; SD = 2.22 years) and 13 older adults (5 male; mean age = 64.00 years; SD = 2.45 years) were included into the statistical analysis. The age ranges of the three groups were restricted to approximately one decade each to assure comparable variance of age across groups. The age groups were matched for their level of education ($\geq$ 14 years of education, see Table 3.1). All participants had normal or corrected-to-normal vision. No participant suffered from any hearing loss (hearing threshold $\leq$ 25 dB as assessed by standard audiometry, Oscilla® SM910-B, Aarhus, Denmark)[2]. No participant was demented (Mini Mental State Examination 2 Score $\geq$ 27; Folstein et al., 2010) or reported any other neurological disease. Prior to the experiment, all participants gave written informed consent. The study was approved by the ethics committee of the University of Leipzig and was conducted in accordance with the Declaration of Helsinki.

Table 3.1: Demographics and Individual Differences (M = mean, SD = standard deviation).

	Age Group						Statistics	
	Young (n=18)		Middle (n=16)		Old (n=13)		*F* *df*(2,44)	*p*
Measure	*M*	*SD*	*M*	*SD*	*M*	*SD*		
Demographics								
Age	24.39	1.30	42.50	2.22	64.00	2.45		
Education	16.83	1.50	19.88	3.13	18.38	2.54	6.56	3.2×10^{-3}
Verbal Intelligence								
Vocabulary Task	53.28	4.76	53.94	5.01	50.00	5.86	2.34	0.11
Similarities Task	27.22	3.25	27.88	3.26	27.69	2.72	0.20	0.83
Composite	0.01	0.66	0.18	0.87	–0.22	0.81	0.96	0.39
Non-verbal Intelligence								
Matrices Task	22.28	1.93	20.69	2.41	17.85	4.16	9.14	4.80×10^{-4}
Block Task	55.67	9.25	53.48	7.74	40.38	9.00	12.88	3.94×10^{-5}
Composite	0.50	0.66	0.16	0.56	–0.88	0.94	14.52	1.43×10^{-5}
Memory								
Digit Span Forward	11.28	2.05	11.19	2.01	9.92	1.93	2.02	
Digit Span Backward	9.72	2.44	8.38	2.19	6.54	1.85	7.84	1.2×10^{-3}
Non-word Repetition Span	27.28	4.62	28.06	2.82	26.62	2.90	0.57	0.57
Counting Span Task	3.56	0.81	3.82	0.82	3.49	0.81	0.68	0.51
Composite	0.16	0.78	0.14	0.70	-0.39	0.57	2.86	0.07
Attention								
Auditory Flanker Task	0.01	0.05	0.05	0.06	0.07	0.06	5.51	7.3×10^{-3}

3.2.2 Standardized Neuropsychological Measures

Sentence processing has been shown supported by several domain-general cognitive functions (e.g., Fedorenko, 2014). To assess possible relations to task-related domain-general cognitive functions, all participants were administered a neuropsychological test battery, measuring working memory (Non-word Repetition Span: Welte, 1981; Counting Span Task: Case et al., 1982; Digit Span Forward/Backward: Aster et al., 2006), auditory attention (Auditory Flankers Task; Chan et al., 2005), verbal intelligence (Similarities and Vocabulary Task),

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[2] For more information on the audiometric assessment, see the Supplements

and non-verbal intelligence (Matrices and Block Tasks; Aster et al., 2006)[3]. Table 3.1 offers an exhaustive overview of age group differences across all neuropsychological test measures.

3.2.3 Stimuli

Accurate comprehension critically relies on the successful encoding of sentences into vWM as sentences unfold. This information often needs to be retrieved at some later point in time. Later retrieval success indirectly reflects encoding success. Our stimulus set addressed these processes in 128 stimuli. Each stimulus was constituted by an encoding sentence, a subsequent retrieval sentence, and a follow-up comprehension question (Table 3.2; as described previously Beese, Meyer, Vassileiou, and Friederici, 2017; Vassileiou et al., 2018. In this design, the retrieval of information from the encoding sentence is triggered by the retrieval sentence, while the retrieval success is subsequently assessed by the comprehension question. That is, the comprehension question directly assessed whether participants successfully retrieved the encoded information. In turn, the comprehension accuracy indirectly reflected on encoding success: Correct responses reflected encoding success, whereas incorrect responses reflected encoding failure. This served as the basis to separate the encoding-related oscillatory power into LR and LNR sentences, the comparison of which yields the SME (Paller et al., 1987; Paller & Wagner, 2002; Werkle-Bergner, Muller, Li, & Lindenberger, 2006). Considering that accurate comprehension relies on successful encoding, it is crucial that the stimulus design discerns memory encoding from language-specific processing efforts. Therefore, in our study, all encoding sentences were of identical syntactic structure while semantic characteristics (e.g., animacy or word frequency) were controlled for. Hence, differences in comprehension accuracy are likely not explained by any language-specific variance, but may instead be related to variance in the encoding success.

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[3] For more information on the neuropsychological tests, see the Supplements

Table 3.2: Experimental Design; examples of encoding sentence, retrieval sentence (requiring retrieval of either subject or object), comprehension question, and feedback.

Phase		Example	
Encoding (5.0–7.8 s, A)		Der Moderator hat den Schriftsteller und die Sängerin angekündigt und die Moderatorin hat den Schauspieler und die Künstlerin angekündigt. *The presenter (m) had announced the writer (m) and the singer (f) and the presenter (f) has announced the actor (m) and the artist (f).*	
		Subject	Object
Retrieval (3.5 s, V)		Die sie Ankündigende war nervös. *The one (f) announcing her was nervous*	Die von ihr Angekündigte war nervös. *The one (f) announced by her was nervous.*
Question (< 4 s, V)	corr	War die Moderatorin nervös? *Was the preseter (f) nervous?*	War die Künstlerin nervös? *Was the artist (f) nervous?*
	gen-l	War die Sängerin nervös? *Was the singer (f) nervous?*	War die Schauspielerin nervös? *Was the actor (f) nervous?*
	cat-l	War die Künstlerin nervös? *Was the artist (f) nervous?*	War die Moderatorin nervös? *Was the presenter (f) nervous?*
Feedback (1.0 s, V)		☺/ ☹	

Note: (f) = female, (m) = male; corr = correct, gen-l = gender lure, cat-l = category-lure; A = Auditory, V = visual

The encoding sentences consisted of two conjoined clauses that each contained one subject and two object noun phrases (see Beese et al., 2017; Vassileiou et al., 2018). All nouns were animate, matched for word length (3–5 syllables) and word frequency (frequency class: 9–19; Goldhahn et al., 2012) within and across sentences. To allow for the encoding of an unambiguous cue for later retrieval, both of the two subject noun phrases across the two clauses (e.g., *der Moderator / the (male) presenter and die Moderatorin / the (female) presenter*) and the object noun phrases within each clause (e.g., first clause: *der Schriftsteller / the (male) writer* and *die Sängerin / the (female) singer*) differed in grammatical gender, which was counterbalanced across stimuli. The specific pairing of two pronouns in the subsequent retrieval sentence unambiguously cued the retrieval of only one specific noun phrase of the encoding sentence. That is, one pronoun referred to only one of the two subjects, while the other pronoun referred to only one of the two objects associated with this subject. For example, in case of an object retrieval, within the retrieval sentence *Die von ihr Angekündigte war nervös (The (female) one announced by her was nervous)*, *ihr* points to the female subject (i.e., *die Moderatorin / the (female) presenter*) and die refers specifically to the female object (i.e., *die Künstlerin / the (female) artist*) associated with this subject. Then, the retrieved noun phrase (i.e., *die Künstlerin / the (female) artist*) can be linked to the adjective (i.e., *nervös/ nervous*). Upon the comprehension question, participants needed to match the previously retrieved information with the information presented during the comprehension question. In 50 % of all trials, the information presented during the comprehension question (e.g., *War die Künstlerin nervös? / Was the (female) artist nervous?*) matched the afore-retrieved correct information (*die Künstlerin / the (female) artist*; CORR). In the other 50 %, the information presented during the comprehension question (e.g., *War die Schauspielerin nervös? / Was the actress nervous?*) mismatched the afore-retrieved correct information (*die Künstlerin / the (female) artist*). Thereby, lure questions were introduced to enforce the encoding of category (category lures; CAT-L; 25 % of trials) and gender information (gender lures; GEN-L; 25 % of trials). Feedback on encoding success was given via a sad or happy emoticon. To counterbalance the distribution of retrieval cues (i.e., grammatical gender of subject and objects) within and across stimuli, eight variants of each stimulus were constructed. Moreover, counterbalancing gender information as well as retrieval type (i.e., subject or object) yielded four variants of the retrieval sentence. Together, this resulted in 32 combinations of the 128 encoding and retrieval sentences, which were distributed via Latin Square across 32 lists. To match processing demands across participants, retrieval type (i.e., subject or object), answer type (i.e., correct or incorrect), and question type (i.e., correct or lure) were balanced across lists.

To avoid habituation and the development of experimental strategies, each list included an additional 64 filler items (adapted from Meyer et al., 2015). To maximize encoding differences relative to the experimental items, fillers were syntactically more complex (i.e., object relative clauses and topicalization constructions) and cued for biological gender (e.g., *uncle – aunt*) instead of grammatical gender. To disguise these differences, syllable count and word frequency were matched to the experimental items. All nouns of experimental and filler items were uniquely used to avoid confounding memory consolidation effects. Stimuli within lists were pseudo-randomized.

3.2.4 Procedure

Data were collected on two days within a single week (mean difference between days = 4.52 days, SD = 2.27 days). On the first day, audiometry and neuropsychological testing were carried out always in the same order (i.e., first audiometry, then Vocabulary Task, Similarity Task, Block Task, Matrices Task, Digit Span Forward, Digit Span Backward, Counting Span Task, and Auditory Flankers Task). On the second day, the electroencephalogram (EEG) was acquired, first at rest (Beese et al., 2017) and then during the experimental task. The EEG was recorded in a dimly lit, electrically shielded, soundproof booth. Here we focus on the EEG recording during the experimental task (see also Vassileiou et al., 2018).

Auditory stimuli (i.e., encoding sentences) were presented via headphones (Sennheiser HD202, Sennheiser GmbH & Co. KG, Wedemark, DE). Audio volume was adjusted to 38 dB above the individual hearing threshold (method of limits; Herrmann, Henry, Haegens, & Obleser, 2016) to ensure an identical hearing level across participants. Visual stimuli (i.e., retrieval sentence, comprehension question and feedback) were presented in white font (Arial, size = 30 pt) against a gray background on a CRT screen 17″, Sony Trinitron Multiscan E220, Sony Corporation, Minato, JP) using Presentation® (Version 17.0, Neurobehavioral Systems, Inc., Berkeley, CA, USA).

Each trial started with the auditory presentation of the encoding sentence which was followed by the visual presentation of the retrieval sentence, the comprehension question, and the feedback (Table 3.2). During the encoding sentence, a fixation cross was visually presented and remained on screen until after a jittered time interval of 1.0–1.5 s. Subsequently, the retrieval sentence was visually presented and followed by another jittered pause of 1.5–2.0 s. A comprehension question followed and needed to be answered within 4 s. Participants responded with ‘yes’ or ‘no’ by pressing the button of one of the two single-button response boxes placed individually under their left and right index finger. Button assignment was counterbalanced across participants. After the response, visual feedback was given for 1 s. A jittered inter-trial interval of 1.5–2.0 s completed each trial. After each block of 32 trials, participants were able to take a break (1–4 min).

This procedure of alternating encoding and retrieval phase has increasingly been used in recent years (e.g., Backus, Schoffelen, Szebenyi, Hanslmayr, & Doeller, 2016; Griffiths, Mazaheri, Debener, & Hanslmayr, 2016), contrary to traditional SME designs that separate encoding and retrieval phase (e.g., Osipova et al., 2006; Paller et al., 1987; Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980; Staudigl & Hanslmayr, 2013; Staudigl, Vollmar, Noachtar, & Hanslmayr, 2015). The decision to alternate the two phases in our study crucially depended on the high information load of each encoding stimulus. That is, each encoding sentence consisted of 19 words that needed to be encoded as syntactically-interrelated semantic information. This degree of information load exceeds that of word pairs (e.g., Haque, Wittig, Damera, Inati, & Zaghloul, 2015; Sanquist et al., 1980; Shing, Brehmer, Heekeren, Bäckman, & Lindenberger, 2016) or word-context pairs (e.g., Griffiths et al., 2016; Staudigl & Hanslmayr, 2013; Staudigl et al., 2015). Therefore, the more immediate retrieval of each encoding sentence, in our study, likely resembles SME designs that delay the retrieval phase to after a block of word pairs. This block of word pairs likely constitutes an information load equivalent to that of the encoding sentence in our study.

3.2.5 Data Acquisition

EEG data were acquired from 63 electrodes at a sampling rate of 1,000 Hz within a passband from DC to 270 Hz. The setup was referenced against the left mastoid and grounded to the sternum. The vertical and horizontal electrooculogram (EOG) was acquired with bipolar electrodes below and above the right eye as well as at the outer canthi of both eyes, respectively. Scalp electrodes were placed according to the international 10–20 system in an elastic cap (WaveGuardTM original, eemagine GmbH, Berlin, DE) connected to a 72-channel Refa8 amplifier (TMS International B.V., Oldenzaal, NL). Electrode impedances were kept below 5 kΩ.

3.2.6 Data Analysis

The EEG data were analyzed with MATLAB® (The MathWorks, Inc., Natick, US), using the FieldTrip Toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). For preprocessing, the data from the encoding sentences were segmented into epochs ranging from –2 s pre-stimulus onset to 7 s post-stimulus onset. EOG data were discarded. First, we high-pass filtered the raw data with a zero-phase finite-impulse-response one-pass 1-Hz Kaiser filter (optimal for independent component analysis, ICA; Winkler, Debener, Muller, & Tangermann, 2015). Then the filtered data were re-referenced to the average of all electrodes to remove any noise from the reference electrode. No channels were excluded or interpolated. Afterwards, muscle contractions, drifts, and jumps were detected based on a semi-automatic, distribution-based approach. First, this procedure involved temporary filtering (110–140 Hz bandpass, 9th order Butterworth filter) of the data and z-transforming those temporarily filtered data per time point across channels. Any trial with greater z-values than 9 at any time point was automatically detected and subsequently visually inspected. Second, all other trials were also visually inspected with respect to their waveform morphology. After this semi-automatic detection, trials that included artifacts were rejected (mean percentage of artifacts rejected = 32.89 %, SD = 15,63 %). For the subsequent ICA, the data were first low-pass filtered to 150 Hz (using a zero-phase finite-impulse-response one-pass Kaiser filter) and then down-sampled to 300 Hz. Second, the mean potential at each electrode was subtracted within trials. Third, a principal component analysis was used to reduce the number of dimensions to finally extract 40 independent components (ICs). ICs reflecting vertical and horizontal eye movement as well as heartbeat were detected upon visual inspection of the components' waveform morphology, power spectrum, and scalp topography (mean number of components rejected = 10.55, SD = 1.78 ICs)[4]. For an optimal statistical analysis of lower oscillatory frequencies, we high-pass filtered the raw data again with a zero-phase finite-impulse-response one-pass 0.1-Hz Kaiser filter[5] and used the information on the artifact trials and components to remove trials with artifacts from these data as well. This 0.1-Hz-filtered data set underwent the same remaining preprocessing steps as mentioned above. Only the 0.1-Hz-filtered data set was used for final data analysis. Afterwards, channels A1 and A2 were removed and the data were re-referenced again to the average of all remaining electrodes. Finally, we visually inspected the data one more time for any remaining artifacts, which were removed accordingly; we then subtracted the mean potential at each electrode within trials.

As the task primarily required participants to decode the syntactic information of the noun phrases (NP; i.e., gender and category information thereof), we extracted the six NPs from the overall encoding sentence (each of which expanded on average over 857 ms, SD = 144 ms). This resegmentation was performed after the data cleaning of the whole

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[4] For a detailed description on the visual detection of the ICs, see the Supplements

[5] For more details on filter-optimized data cleaning, see the Supplements

encoding sentence in order to guarantee clean data for all six NPs. The resegmentation was based on the available EEG triggers which were set in close approximation to the NPs. These resulting new segments crucially always included the noun phrase at their core. For instance, the encoding sentence *Der Moderator hat den Schriftsteller und die Sängerin angekündigt und die Moderatorin hat den Schauspieler und die Künstlerin angekündigt (The (male) presenter had announced the (male) writer and the (female) singer, and the (female) presenter had announced the (male) actor and the (female) artist) was resegmented into "der Moderator hat/ the (male) presenter had", "den Schriftsteller und/ the (male) writer and", "die Sängerin/ the (female) singer", "die Moderatorin hat/ the (female) presenter had", "den Schauspieler und/ the (male) actor and" and "die Künstlerin/ the (female) artist".* This resegmentation created a time series of six NPs per sentence. Crucially, it optimized the statistical analysis as the NPs were now well-aligned across stimuli (for further information on this analysis step,see Vassileiou et al., 2018).

Using a Hann taper, frequency analysis via a Fast-Fourier Transform was performed upon each NP in steps of 0.5 Hz from 2–40 Hz with a spectral smoothing of 1 Hz. As the length of the NPs varied between 492ms and 1321 ms (mean = 857ms; SD = 144ms), equal frequency resolution across all NPs was achieved by zero padding the signal of all NPs to 2 s. After frequency analysis, the signal across all NPs of each sentence position was averaged separately for LN and LNR sentences, yielding six power estimates per condition, per channel–frequency pair and per participant. Subsequently, per participant, these power estimates were baseline corrected relative to a condition-specific pre-stimulus baseline window ranging from –1 to 0 s (corrected signal = (signal – baseline) / baseline)[6]. Thereby, the baseline signal was first zero padded to 2 seconds to match the length of the NPs. Then the baseline signal was averaged across time, per channel-frequency pair, and subtracted from the signal of each NP and then divided by the averaged baseline signal. The baseline signal did not differ between LN and LNR sentences ($z = 0.31$, $p = 0.76$). The choice of baseline correction method is based on our previously published study (Vassileiou et al., 2018), enabling a comparison of results between studies.

3.2.7 Statistical Analysis

The comprehension accuracy was quantified using d-prime scores (d′) which indirectly indicated encoding success. Compared to traditionally used percentage correct measures, d'-scores have the advantage of controlling for participants' response bias (i.e., the indi-

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[6] For a detailed discussion on the choice of the baseline correction method, see the Supplements

vidual tendency for responding *'yes'* or *'no'*). D′scores were computed by subtracting the z-transformed false alarm rate (FA) from the z-transformed hit rate (H). FA or H of 0 was corrected by 1/N and FA or H of 1 was corrected by (N–1)/N (N = number of trials; Macmillan & Creelman, 2005). In a first step, any participant whose sensitivity to the task was below chance (i.e., $d' \leq 0$ and/or accuracy < 50 %) was excluded from further statistical analyses, as the associated EEG signal cannot be assumed to reflect encoding success. This resulted in the exclusion of 11 from the original 59 participants: 2 younger, 2 middle-aged, and 7 older adults. One additional middle-aged adult was excluded from further statistical analyses as the clean data contained fewer than 10 LNR trials (Scholz, Schneider, & Rose, 2017).

The comprehension accuracy was used as an index of encoding success. Specifically hits and correction rejections (i.e., correct responses) reflected LR sentences, which indirectly indicated encoding success. In contrast, misses and false alarms (i.e., incorrect responses) reflected LNR sentences, which indirectly indicated encoding failure. This classification deviates from that of previous studies, in which only hits define LR trials and only misses define LNR trials. However previous designs compared old (i.e., accessible from memory) with new (i.e., inaccessible from memory) items at the retrieval. In contrast, in our design we contrasted old information that matched the information in the comprehension question with old information that mismatched the information in the comprehension question. Hence, the retrieved information was always accessible in case that it was successfully encoded. Therefore, correct rejections indicate encoding success as much as hits, and false alarms indicate encoding failure as much as misses. On average, participants had 59 LR trials and 26 LNR trials left after artifact rejection, which is comparable to the LR–LNR ratio of previous SME studies (70% LR – 30% LNR; e.g., Gruber, Tsivilis, Montaldi, & Muller, 2004; Hanslmayr et al., 2011; Meeuwissen, Takashima, Fernandez, & Jensen, 2011; Staudigl & Hanslmayr, 2013) guaranteeing above-chance performance as well as roughly comparable numbers of trials per condition. We refrained from bootstrapping LR trials to match the number of LNR trials, as it was previously shown that this would not change the SME (Staudigl & Hanslmayr, 2013).

Conventionally classified frequency bands of theta (4–8 Hz), alpha (8–12 Hz) and beta (15–30 Hz) were adjusted to the individual alpha peak frequency (IAF; for further details, see Beese et al., 2017) because of substantial inter-individual variance of the IAF across age groups (YA mean peak = 10.58 Hz, *SD* = 0.77 Hz; MA mean peak = 10.31 Hz, *SD* = 1.04 Hz; OA mean peak = 9.77 Hz, *SD* = 0.04 Hz; $F(2,46) = 3.33$, $p = 0.04$; Köpruner, Pfurtscheller, and Auer (1984))—optimizing the interpretation of the frequency bands' functional significance. The theta band is adjusted as it has been shown to vary as a function of the individual alpha band frequency, dissociating phasic theta synchronization from alpha desynchronization (e.g., Klimesch, 1999), while beta has previously been shown to have a harmonic relationship with alpha (e.g., Carlqvist, Nikulin, Stromberg, & Brismar, 2005). We adjusted the theta range from IAF–6 to IAF–2, the alpha range from IAF–2 to IAF+2 and the beta range from IAF+5 to IAF + 20 (adapted from Klimesch, 1999). We additionally divided the alpha band into a lower (IAF–2 to IAF) and an upper alpha band (IAF to IAF +2) as Klimesch (1999) has suggested distinct functional relevance of lower and upper alpha. That is, lower alpha (i.e., 8–10 Hz) is associated with attention, while upper alpha (i.e., 10–12 Hz) is related to memory performance.

For sensor-level statistics we averaged the oscillatory power within each frequency band (i.e., for the theta, lower and upper alpha, as well as beta band) across all NPs, within participants. Within each frequency band and electrode, oscillatory power was subjected to a repeated-measures analysis of variance (rANOVA) with the between-subjects factor age group (levels: younger, middle-aged, and old) and the within-subjects factor encoding success (levels: LR and LNR). Within frequency bands, across electrodes, p-values were FDR-corrected for multiple comparisons. Any interaction effects were dissolved using FDR-corrected simple-effects analyses.

To examine the domain-specificity of the effects post-hoc, we first correlated the cognitive abilities assessed by the neuropsychological test battery with the sentence comprehension accuracy. To this end, the neuropsychological test scores were first z-transformed and averaged within participants across age groups into composite scores reflecting (see Standardized neuropsychological measures): memory (Cronbach's $\alpha = 0.70$), non-verbal intelligence (Cronbach's $\alpha = 0.78$), verbal intelligence (Cronbach's $\alpha = 0.33$) and attention. We then related those cognitive abilities that were associated with sentence comprehension accuracy to age-related SME differences. To this end, we averaged oscillatory power within the lower alpha band across those electrodes for which there were age differences in the SME (see Results). Then, separate repeated-measures analyses of covariance (rANCOVA) were computed with the factors age group and encoding success as well as the respective composite score as between-subject covariate. We reasoned that if any of the composite scores relate to the interaction between age group and encoding success, this alpha effect may be additionally explained by other general cognitive functions.

3.3 Results

The behavioral data showed clear age differences ($F(2,46) = 10.88$, $p = 0.0001$; Figure 3.1), with better performance in younger and middle-aged adults compared to older adults. Younger adults remembered on average 73.62 % (*SD* = 7.00 %) of all sentences correctly (mean d$'$= 1.33, *SD* = 0.45). Middle-aged adults remembered 69.03 % (*SD* = 8.88 %) of all trials correctly (mean d$'$= 1.07, *SD* = 0.54). Older adults remembered 60.17 % (*SD* = 7.07) of all trials correctly (mean d$'$= 0.53, *SD* = 0.39). Group performances exceeded chance level for all age groups (one-sample t-test on d$'$ within age group; all $t > 4.88$, all $p < 0.001$).

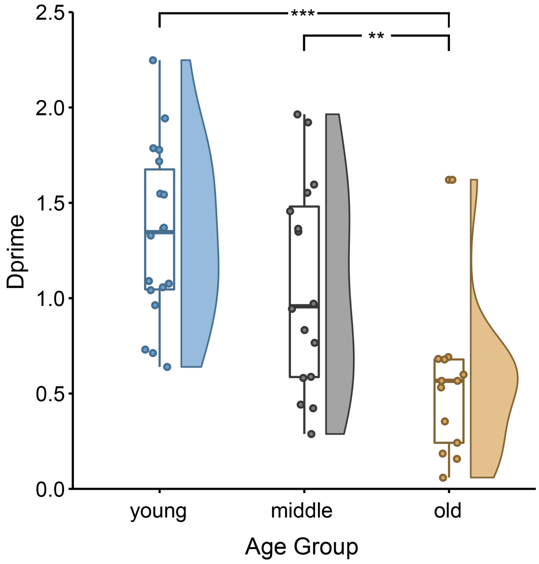

Figure 3.1: Lower sentence comprehension accuracy, indirectly indicating lower encoding success, for older than younger and middle-aged adults: single subject means (scatter points), group medians (line within boxes), as well as probability density of d-prime values of younger, middle-aged and older adults.

The rANOVAs at each electrode showed an age dependence of the SME for the lower alpha band—but not for the theta, upper alpha or beta band. Specifically, the interaction effect between age group and encoding success was significant at bilateral frontal and right-hemispheric parietal sites (all $4.30 < F(2,44) < 7.44$; all $2.13 \times 10^{-2}) < p < 4.79 \times 10^{-2}$), FDR-corrected; all $0.03 < \eta < 0.08$; Figure 3.2). There was no main effect of age (all $0.06 < F(2,44) < 3.51$; all $7.36 \times 10\text{–}1 < p < 9.38 \times 10^{-1}$), FDR-corrected) or of encoding success (all $0.01 \times 10^{-5}) < F(1,44) < 8.80$; all $2.95 \times 10^{-1}) < p < 9.21 \times 10^{-1}$), FDR-corrected).

Simple-effects analyses revealed consistent age differences between younger and older adults in the overall SME (i.e., LR–LNR; all $3.55 \times 10^{-4} < p < 1.51 \times 10^{-2}$, FDR-corrected;

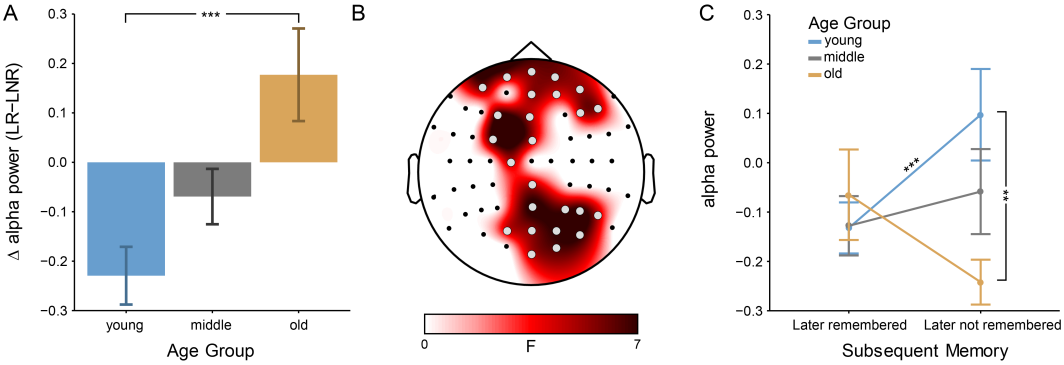

Figure 3.2: Subsequent memory effect (SME) across age groups: (A) Encoding-related power decreases in younger adults (i.e., lower power for later-remember (LR) than for later-not-remembered (LNR) sentences), averaged across all significant electrodes (shown in B) within the lower alpha band (i.e., individual alpha peak frequency (IAF) – 2 Hz to IAF) are attenuated in middle-aged adults and turn into a power increases in older adults; error bars reflect one standard error; *** $p < .001$ (B) Scalp topography shows that the age difference in the SME within the lower alpha band is distributed across bilateral frontal and right-hemispheric parietal sites (gray electrodes: $p < .05$, FDR-corrected), (C) Interaction effect between age groups and encoding success: lower alpha power differs between younger and older adults for LNR but not LR sentences; *** $p < .001$; ** $p < .05$.

Figure 3.2A) at all electrodes for which the interaction effect between age group and encoding success was significant (Figure 3.2B). At a closer look, age-related SME differences between younger and older adults were actually only related to age differences in the power underlying LNR but not LR sentences (at F3, FC3, P6, PO4, PO6, PO8 and O2; all $3.85 \times 10^{-3} < p < 1.01 \times 10^{-2}$, FDR-corrected; Figure 3.2C).

Within age groups, only younger adults showed a significant difference in encoding-related oscillatory power (i.e., LR–LNR; all $4.87 \times 10^{-5} < p < 3.13 \times 10^{-2}$, FDR-corrected; at FP2, AF8, Fz, F3, FC3, FCz, C1, CPz, Pz, P4, P6, P8, POz, PO4, PO8 and O2; Figure 3.3). Specifically, younger adults showed a negative SME (i.e., LR $<$ LNR). This effect was numerically, though not significantly, attenuated in the middle-aged adults. This turned into a numerical, though not significant, positive SME in the older adults (i.e., LR $>$ LNR).

Post-hoc, we found that sentence comprehension was associated both with working memory ($r = 0.52$, $p = 3.75 \times 10^{-4}$, FDR-corrected) and non-verbal intelligence ($r = 0.52$, $p = 3.75 \times 10^{-4}$, FDR-corrected) across age groups. Both, working memory and non-verbal intelligence differed across age groups (see Table 3.1). Therefore, further post-hoc analyses were conducted to test the domain-specificity of age-related SME differences. The results revealed that while both working memory and non-verbal intelligence associated with sentence comprehension, age differences therein did not associate with age-related SME differences (all $0.04 < F(2{,}41) < 5.08$; all $0.27 < p < 0.96$; FDR-corrected).

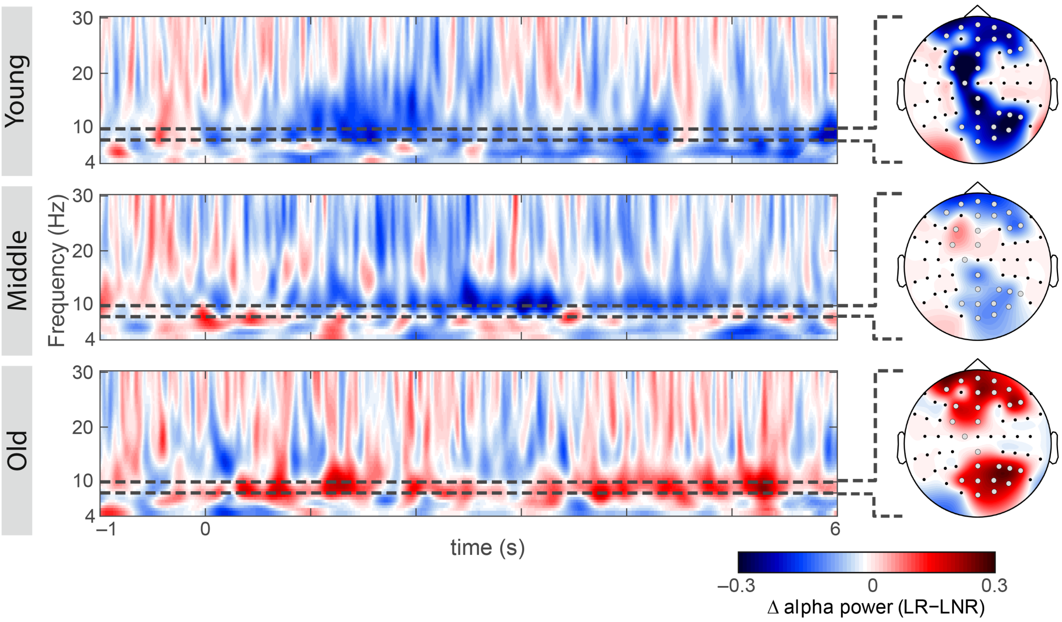

Figure 3.3: Subsequent memory effect within each age group at electrodes of group-level significance (as shown in B): oscillatory power differences between later-remember (LR) than for later-not-remembered (LNR) sentences across the theta, alpha and beta frequency range (4 – 30Hz) across the minimum sentence length, including the baseline window (–1 to 6s) for younger, middle-aged and older adults; scalp topographies showing encoding-related lower alpha power differences between LR and LNR (gray electrodes indicate group-level significance). All spectra and topographies were adjusted for the individual alpha peak.

3.4 Discussion

This study gives first indications that older adults' sentence comprehension difficulties may be related to age differences in oscillatory patterns underlying sentence encoding. We found encoding-related age differences between younger, middle-aged, and older adults in lower alpha-band power. Specifically, comparing encoding-related alpha power between LR and LNR sentences, younger adults displayed a negative SME (i.e., LR $<$ LNR), which was attenuated in the middle-aged adults and shifted towards a positive SME in older adults (i.e., LR $>$ LNR). Age differences in the SME were dominated by differences between younger and older adults in the power underlying LNR, but not LR sentences. That is, when older adults failed to encode sentences, the oscillatory pattern was reversed; but when older adults successfully encoded sentences, the oscillatory pattern matched that of younger adults. We tentatively suggest that age-related sentence comprehension difficulties are associated with age differences in sentence encoding.

With alpha band power having been previously related to inhibitory processes, the lifespan shift from an alpha-band power decrease to an alpha-band power increase may reflect a functional shift from cortical disinhibition to inhibition (e.g., Jensen & Mazaheri, 2010).

While increased alpha-band power has been proposed to inhibit task-irrelevant regions, decreased alpha-band power is supposed to gate the information flow towards task-relevant regions (Haegens, Osipova, Oostenveld, & Jensen, 2010; Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007). Following this train of thought, alpha-band oscillations are often thought to regulate the information flow through the cortex. Specifically, task-irrelevant information is suppressed when alpha power increases (Hanslmayr et al., 2011; Jensen & Mazaheri, 2010; Palva, Palva, & Kaila, 2005; Sauseng, Klimesch, Gerloff, & Hummel, 2009; Zanto & Gazzaley, 2009), while task-relevant information is enhanced when alpha power decreases (Babiloni et al., 2004; Hartmann, Schlee, & Weisz, 2012; Hauck, Domnick, Lorenz, Gerloff, & Engel, 2015). Therefore, successful encoding in younger adults may be supported by the enhancement of task-relevant information through cortical disinhibition, as reflected by decreased alpha power. Older adults' difficulties in the processing of vMW-taxing sentences may be associated with an age-related inefficiency in cortical disinhibition.

As sentences unfold, upcoming information interferes with already encoded information (Lewis, Vasishth, & Van Dyke, 2006). The ability to inhibit interfering information is thus a critical determinant of successful sentence comprehension (e.g., Glaser, Martin, Van Dyke, Hamilton, & Tan, 2013; Lewis et al., 2006; Santi, Friederici, Makuuchi, & Grodzinsky, 2015; Van Dyke, 2007). Age deficits in this ability to inhibit interfering information may compromise sentence processing (Hasher & Zacks, 1988). In support, in our study, when sentences were later not remembered (i.e., LNR sentences), alpha power was found lower in older than younger adults. Linking alpha power to inhibition, this may reflect inhibitory deficits in older adults. In contrast, when sentences were later remembered (i.e., LR sentences), alpha power did not differ between age groups. Hence, age-related SME differences are predominantly driven by encoding failure (i.e., LNR sentences) rather than encoding success (i.e., LR sentences). However, when comparing encoding success to encoding failure, it appears that younger and older adults rely on opposing processes (i.e., negative versus positive SME). That is, in comparison to encoding failure, younger adults may achieve encoding success through cortical disinhibition (i.e., alpha power LR $<$ LNR). In contrast, older adults may achieve encoding success through cortical inhibition (i.e., alpha power LR $>$ LNR). Hence, successful encoding may rely on a disinhibition-to-inhibition shift across the lifespan. In this vein, previous studies showed that older adults remain able to enhance task-relevant information (Gazzaley et al., 2008; Radvansky, Curiel, Zwaan, & Copeland, 2001). Such a decrease in inhibition allows for increased distractibility (Lavie, Hirst, de Fockert, & Viding, 2004) which overloads older adults' limited vWM capacity storage (Vogel, McCollough, &

Machizawa, 2005). This in turn affects their memory performance (Eriksen & Eriksen, 1974; Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Zanto & Gazzaley, 2009). Therefore, a lifespan shift from disinhibition-to-inhibition may be a mechanistic substrate of age differences in sentence encoding underlying age-related sentence comprehension difficulties.

This lifespan shift from disinhibition to inhibition may also indicate an age-related shift from bottom-up to top-down processing. That is, disinhibiting detailed sentence information may imply a bottom-up extraction of such information. In contrast, inhibiting the information may imply a top-down extraction of fewer details, focusing on gist information. While our results suggest younger adults' encoding success to be related to the disinhibition of information, older adults' encoding success may be linked to the inhibition of information. Accordingly, lower alpha power underlying encoding success has been associated with bottom-up encoding in younger adults (Hanslmayr, Staudigl, & Fellner, 2012). In contrast, older adults have been shown deficient in bottom-up processing (Madden, 2007; Madden, Whiting, & Huettel, 2005; Wingfield, Aberdeen, & Stine, 1991). In line with this, older adults also show greater alpha power related to encoding success than younger adults (Karrasch et al., 2004). In addition, it has been noted that older adults do not extract rich and detailed information, but rather the overall gist of sentences when sentences were accurately comprehended (Christianson, Williams, Zacks, & Ferreira, 2006; Tun, Wingfield, Rosen, & Blanchard, 1998). Together with our results this may suggest that older adults can successfully encode sentences through top-down processing (Whiting, Madden, & Babcock, 2007; Whiting, Sample, & Hagan, 2014; Wingfield et al., 1991). However, in our study, the task required a bottom-up, word-by-word encoding of detailed syntactic information; top-down encoding would have been insufficient to successfully solve the task at hand. This may explain our observation that older adults showed lower performance accuracy.

One might expect that age differences in sentence encoding may be associated with age differences in domain-general cognitive abilities that are known to support sentence comprehension (Beese et al., 2017; Fedorenko, 2014; Hoffman & Morcom, 2018). That is, an age-related decrease in vWM capacity (e.g., Bopp & Verhaeghen, 2005)or attention (e.g., Madden, 2007; Madden et al., 2005) may link to the employment of gist extraction in older adults (Christianson et al., 2006; Ferreira & Patson, 2007; Tun et al., 1998). While our post-hoc analyses showed that sentence comprehension is generally supported by domain-general cognitive abilities, we did not observe any relation between those domain-general cognitive abilities and the encoding-related oscillatory differences between age groups.

3.5 Limitations

One obvious limitation of this study is the small sample size of the individual age groups. However, our previously published study (Vassileiou et al., 2018) showed that the SME effect for this design is already reliable at a small sample size, that is, 22 participants (effect size (dz) = –0.81), as estimated by a power analysis (Faul, Erdfelder, Buchner, & Lang, 2009). However, after data cleaning the current data set includes only 18 younger, 16 middle-aged and 13 older adults. Even though the effects of this study are likely underpowered, they contribute to the field by providing a tentative link between age-related sentence comprehension difficulties and encoding-related electrophysiological dynamics. Future studies should include a sufficient number of participants in each group, focusing on younger and older adults only, as the current effect was linear across the lifespan.

Moreover, another concern regards the signal-to-noise ratio (SNR). The SNR of encoding-related activity decreases across the lifespan with diminishing retrieval confidence (e.g., Cansino et al., 2010; Friedman & Trott, 2000; Gutchess, Ieuji, & Federmeier, 2007; Kamp & Zimmer, 2015). High retrieval confidence is associated with recollection-based memory (i.e., "remember" responses; Tulving, 1985) while lower retrieval confidence is associated with familiarity-based memory (i.e., “know” responses; Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998). Older adults produce fewer recollection-based and equal or more familiarity-based responses compared to young adults (e.g., Friedman, Nessler, & Johnson Jr, 2007; Friedman & Trott, 2000; Mark & Rugg, 1998). Previous studies found age differences in the encoding-related signal primarily when the information was retrieved with high confidence. That is, at high confidence, the magnitude of the SME is reduced in older compared to younger adults (Friedman & Trott, 2000; Gutchess et al., 2007; Kamp & Zimmer, 2015) while also onset and topography differs across age groups (Cansino et al., 2010). Such age-related SME differences may disappear when high and low retrieval confidence is not discerned (Gutchess et al., 2007). As we did not assess retrieval confidence, the SNR in our data may be reduced in older compared to younger adults. This may be the reason why encoding-related differences between LR and LNR were just numerical and not significant in older adults while the SME was clearly significant in younger adults.

3.6 Conclusion

Our study contributes to the understanding of neurocognitive aging, especially in the field of sentence processing. We here addressed the question whether age-related sentence comprehension difficulties associate with age differences in the neural correlates underlying sentence encoding. The results provide initial evidence for a lifespan shift from decreased to increased encoding-related alpha power, which likely reflects a shift from cortical disinhibition to inhibition. That is, in comparison to encoding failure, encoding success is achieved through decreased alpha power in younger adults, reflecting cortical disinhibition, and increased alpha power in older adults, reflecting cortical inhibition. Disinhibition may entail bottom-up information processing while inhibition may entail top-down information processing. Overall, our results suggest that age-related sentence comprehension difficulties are not only language-specific but may also associate with memory encoding-related electrophysiological alternations across the lifespan.

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Chapter 4

Study 3

Adult age differences in the benefit of syntactic and semantic constraints for sentence processing[1]

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Published in Psychology and Aging in 2019

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[1] This chapter is adapted from the article published in Psychology and Aging by Beese, Werkle-Bergner, Lindenberger, Friederici, and Meyer (2019)

Abstract

Verbal working memory-intensive sentence processing declines with age. This might reflect older adults' difficulties with reducing the memory load by grouping single words into multi-word chunks. Here we used a serial order task emphasizing syntactic and semantic relations. We evaluated the extent to which older compared to younger adults may differentially use linguistic constraints during sentence processing to cope with verbal working memory limitations. Probing syntactic-semantic interactions, age differences were hypothesized to be confined to the use of syntactic constraints and to be accompanied by an increased reliance on semantic information. Two experiments varying in verbal working memory demands were conducted: the sequence length was increased from eight items in Experiment 1 to eleven items in Experiment 2. We found the use of syntactic constraints to be compromised with aging, while the benefit of semantic information for sentence processing was comparable across age groups. Hence, we suggest that semantic information processing may become relatively more important for successful sentence processing with advancing adult age, possibly inducing a syntactic-to-semantic-processing strategy shift.

Keywords: Aging; chunking; semantics; syntax; working memory

4.1 Introduction

It is widely debated whether language processing declines with age (for review see Shafto & Tyler, 2014). While aging has been argued to spare the processing of short or simple sentences (e.g., Gilchrist, Cowan, & Naveh-Benjamin, 2008; Wingfield, Poon, Lombardi, & Lowe, 1985), the processing of long or complex sentences deteriorates with age (e.g., Feier & Gerstman, 1980; Kemper, 1987; Obler, Fein, Nicholas, & Albert, 1991). This may be related to an age-related decline in verbal working memory (vWM; e.g., Beese, Meyer, Vassileiou, & Friederici, 2017; Bopp & Verhaeghen, 2005; Salthouse, 1994) as both long and complex sentences tax vWM (Gibson, 2000; Just & Carpenter, 1992; Meyer, Obleser, Kiebel, & Friederici, 2012). The present study investigated whether older adults exploit specific linguistic constraints, that is syntactic regularities and semantic relations, to different extents in order to counteract their reduced vWM capacities when sentence processing becomes difficult.

Syntactic and semantic constraints on sentence processing have been shown to be employed differentially across the life span (e.g., Friederici, Schriefers, & Lindenberger, 1998). Comparing syntactic and semantic processing directly, it was found that syntactic, but not semantic processing, was deficient in older, relative to younger adults (Friederici et al., 1998). Other studies investigating either syntactic or semantic processing in elderly people support this finding: syntactic processing speed and accuracy are lower in older compared to younger adults when processing demands are high. That is, for example, when processing syntactically long, ambiguous or complex sentences (e.g., Kemper, 1986; Kemper, Crow, & Kemtes, 2004; Obler et al., 1991, respectively). In comparison, lexical-semantic processing speed and accuracy do not appear to differ between younger and older adults (e.g., Burke, White, & Diaz, 1987; Gunter, Jackson, & Mulder, 1998; Laver, 2009). In addition, the results of numerous studies document adult age differences in online sentence processing heuristics during self-paced reading (e.g., Radvansky, 1999; Radvansky, Curiel, Zwaan, & Copeland, 2001; Radvansky & Dijkstra, 2007; Stine-Morrow, Loveless, & Soederberg, 1996; Stine-Morrow, Noh, & Shake, 2010; Stine, 1990). Specifically, older adults allocate fewer resources than younger adults to the decoding of orthographic or syntactic features (i.e., the surface form) or to the conceptual integration of words into coherent syntactic constituents conveying propositional content (i.e., the textbase). Rather, older adults focus on the creation of the mental representation of the events described (i.e., the situation model). Hence, older adults may rely more on semantic than syntactic constraints in order to successfully process sentences.

Insufficient resources, in particular verbal working memory limitations as a domain-general processing resource (Gibson, 2000; Just & Carpenter, 1992; Meyer et al., 2012), may impair older adults' engagement in enriched sentence processing (e.g., Christianson, Williams, Zacks, & Ferreira, 2006). Generally, the verbatim surface form and textbase information (i.e., syntactic regularities and propositional content, respectively) are remembered for shorter intervals than the situation model of sentences (i.e., the overall event described; Kintsch, Welsch, Schmalhofer, & Zimny, 1990; Sachs, 1967). Particularly, in older adults, representations of surface form or textbase information fade away even more rapidly (e.g., Radvansky et al., 2001). Hence, it seems plausible to assume that advancing adult age is accompanied by a shift in processing heuristics. According to this proposal, older adults allocate fewer resources to an enriched decoding of surface form or textbase information, and more resources to the situation model than younger adults (e.g., Stine-Morrow et al., 1996). This processing heuristic may help older adults to reduce demands on resources that would otherwise be unavailable if already consumed by these lower level processes.

Syntactic and semantic constraints can be helpful to reduce vWM costs during sentence processing. That is, discrete words can be grouped into multi-word phrases based on syntactic regularities and semantic relations (e.g., Bonhage, Meyer, Gruber, Friederici, & Mueller, 2017; Epstein, 1962). This grouping, henceforth chunking, increases the amount of information stored in working memory (Gilchrist & Cowan, 2012; Gobet et al., 2001; Gobet, Lane, & Lloyd-Kelly, 2015; Miller, 1956). On the one hand, words can be grouped together on the basis of syntactic regularities (e.g., word categories, word order), for example, the function word *"the"* with the content word *"boat"* into the multi-word phrase *"the boat"* (e.g., Bonhage et al., 2017; Meyer, Henry, Gaston, Schmuck, & Friederici, 2017; Schell, Zaccarella, & Friederici, 2017). When words are grouped together by syntactic regularities, they are remembered better than words that cannot be grouped together in this way (the so-called sentence superiority effect, e.g., Baddeley, Hitch, & Allen, 2009; Bonhage, Fiebach, Bahlmann, & Mueller, 2014; Bonhage et al., 2017; Cattell, 1886; Snell & Grainger, 2017). From now on, we call this grouping process syntactic chunking. The term denotes the abstract binding of words' syntactic categories, which has been argued to occur rather automatically, unconsciously, and without any strategic efforts (Baddeley et al., 2009; Freudenthal, Pine, Aguado-Orea, & Gobet, 2007; Gobet, Lloyd-Kelly, & Lane, 2016). In the above example, the binding of *"the"* and *"boat"* is based on syntactic not semantic information, creating a two-word phrase without building up a semantic representation that would go beyond the word-level meaning. Similarly, multiple content words like *"sleepy"* and *"boat"* may also be grouped together based on syntactic information. However, this can result in a semantically anomalous phrase, like *"sleepy boat"*, when the content words are not semantically related. But when words can indeed be grouped together based on semantic information (e.g., semantic relatedness), then enriched semantic representations are formed. For example, the content words *"wooden"* and *"boat"* may be grouped together into one joint representation of a *"wooden boat"* creating an enriched semantic representation of *"boat"* (Schell et al., 2017). This is conventionally known as conceptual chunking (Bierwisch & Schreuder, 1992; Miller, 1956).

Age differences in the chunking of word sequences have been found in studies examining either online, real-time processing (for an overview see, Stine-Morrow & Payne, 2016) or post-stimulus, offline effects (Gilchrist et al., 2008); yet, the online and offline results differ. On the one hand, online studies suggest that older adults generate smaller chunks to accommodate their vWM capacity limitations, reflected in a greater allocation of processing resources to intra-sentence as compared to inter-sentence boundaries (e.g., Stine-Morrow et al., 2010; Stine, 1990). On the other hand, offline studies suggest that older adults remember fewer, but not smaller chunks than younger adults. For instance, Gilchrist et al. (2008) manipulated both memory load (i.e., number of unrelated sentences) and chunk size (i.e., number of clauses), reporting age differences during verbatim recall with respect to the former but not to the latter. There are several relevant differences between previous online and offline studies. First, online and offline studies assessed chunking differently: online studies inferred chunking on the basis of reading or gaze time measurements, while offline studies assessed chunking by enhancing or reducing opportunities for chunking in the experimental material. Second, online studies dissociated syntactic and semantic information processing via statistical means, rather than via experimental manipulations; the offline studies did not dissociate the contribution of these distinct linguistic information types on chunking at all. However, no study to date has assessed age differences in the extent to which different linguistic information types are used for chunking, neither online nor offline. To clarify this open question, our study aimed at dissociating the extent to which older adults differentially use syntactic and semantic constraints for chunking during sentence processing to circumvent their vWM limitations, using an offline task.

Syntactic chunking has been shown to occur independently of semantic information processing in younger adults (Epstein, 1962); however, this may change with increasing syntactic processing deficits across the life span. Here, we manipulate the availability of syntactic and semantic constraints for chunking during sentence processing in younger and older adults. We employed sentences that pose lower (Experiment 1) or higher (Experiment 2) vWM demands through varying the sequence length. Syntactic chunking was assessed through the classical comparison of multi-word syntactic phrases versus random word lists (Baddeley et al., 2009). To assess semantic information processing, we adapted the classical dissociation of meaningful versus meaningless words by comparing real words to pseudowords (e.g., Cattell, 1886; Epstein, 1962; Reicher, 1969). We used an offline serial order task to assess processing success for verbal materials that vary in the availability of syntactic and semantic constraints. The presence of those linguistic constraints facilitated or hampered chunking and therefore the accommodation of vWM limitations. We hypothesized that older adults do not use syntactic constraints as much as younger adults during the processing of longer sentences, as vWM-intensive sentence processing is known to deteriorate with age (e.g., Kemper, 1986; Kemper et al., 2004; Obler et al., 1991). Furthermore, due to this disadvantage in syntactic chunking, we expected a stronger reliance on semantic constraints in older participants. This is in line with previous studies suggesting a syntactic-to-semantic processing strategy shift in the elderly (e.g., Amichetti, White, & Wingfield, 2016). Systematically varying the availability of syntactic and semantic constraints during sentence processing, the results showed that the advantage of remembering the temporal order of words in sentences over lists was reduced in older compared to younger adults, in particular when sentences were longer, and thus highly vWM-demanding (Experiment 2). This observation indicates that syntactic constraints may not be used as much by older as compared to younger adults. While the presence of syntactic constraints was more beneficial for younger than older adults, the benefit of the presence of semantic constraints was comparable across age groups.

4.2 Experiment 1

Previous literature suggests that older adults have difficulties processing vWM-intensive sentences (e.g., Beese et al., 2017; Kemper, 1986, 1987; Wingfield et al., 1985). The extent to which the presence of syntactic regularities benefits vWM-intensive sentence processing, by enabling syntactic chunking und thereby reducing the vWM load, can be indexed through the sentence superiority effect (Baddeley et al., 2009). Age differences in the sentence superiority effect have been found more pronounced in eight-word sequences (Wingfield et al., 1985). Specifically, it has been shown that older adults repeat five– and eight-word sentences as accurately as younger adults. However, older but not younger adults' repetition accuracy is poorer for eight-word, but not five-word lists. Therefore, in Experiment 1, meaningful and meaningless lists and sentences of eight words were compared. We aimed at dissociating the contribution of syntactic from semantic constraints to age differences in sentence processing.

4.2.1 Methods

Participants

56 healthy right-handed native speakers of German, divided into two equally-sized age groups (younger versus older adults), participated for a reimbursement of 9 € per hour. After outlier removal (see Experiment 1 – Statistical analysis), the data of 27 younger adults (13 males, age range = 20 – 31 years, mean age = 25.67 years, standard deviation (SD) age = 2.56 years) and 26 older adults (12 males, age range = 62 – 71 years, mean age = 66.35 years, SD age = 2.40 years) were analyzed. The age ranges of the two groups were restricted to approximately one decade each to assure comparable variance of age across groups. All participants had normal or corrected-to-normal vision and did not suffer from any neurological disorders according to self-report. The age groups were matched for their level of education (i.e., they had at least a high-school diploma or an equivalent; for more details see Table 4.1). Prior to the experiment, all participants gave written informed consent. The experiment was approved by the ethics committee of the University of Leipzig. The experiment was conducted in accordance to the Declaration of Helsinki.

Verbal Working Memory Measures

To assess potential associations of age differences in vWM with sentence processing (e.g., Bopp & Verhaeghen, 2005; Lewis, Vasishth, & Van Dyke, 2006; Salthouse, 1994), we acquired three additional standardized measures. Two of those measured particularly the storage component of vWM, or otherwise short-term memory capacity(i.e., the digit span task forward Aster, Neubauer, and Horn, 2006; and the non-word repetition span task Welte, 1981. One further test assessed both the storage as well as the manipulation component (i.e., the digit span task backward Aster et al., 2006).

Table 4.1: Demographics and Individual Differences – Summary of Experiment 1 & 2.

	Experiment 1						Experiment 2					
	Young (n = 27)		Old (n = 26)		t	p	Young (n = 26)		Old (n = 27)		t	p
Measure	M	SD	M	SD			M	SD	M	SD		
Demographics												
Age	25.67	2.56	66.35	2.40			25.12	3.24	64.19	2.76		
Education	17.56	1.99	17.92	1.98	−0.67	.50	18.08	2.76	16.63	2.45	2.02	.05
Memory												
digit span forward	10.81	2.29	9.85	1.59	1.79	.08	10.73	1.43	9.59	1.82	2.53	.01
digit span backward	8.70	2.27	6.15	1.54	4.80	1.70×10^{-5}	8.62	2.55	6.59	1.42	3.55	1.02×10^{-3}
repition span	27.93	3.00	25.62	3.59	2.54	.01	26.69	3.33	25.15	4.83	1.36	.18
repetition span	27.93	3.00	25.62	3.59	2.54	.01	26.69	3.33	25.15	4.83	1.36	.18
composite score	0.37	0.72	−0.38	0.66	3.94	2.5×10^{-4}	0.33	0.73	−0.37	0.77	3.11	3.0×10^{-3}

Given that the three tests of vWM showed a moderate degree of common variance (α = 0.69), we combined the test scores into one composite score (see Experiment 1 – Statistical analysis). The test results are reported in Table 4.1. For 18 participants (12 younger, 6 older adults), these tests were acquired for the current study in this order; for all other participants, the test results were available from a previous study (mean delay = 13 months; *SD* delay = 1 month; Beese et al., 2017).

Stimuli

The study design followed a 2 × 2 design with the factors sentence structure (sentences versus word lists) and meaning (real words versus pseudowords; see Table 4.2). Stimuli consisted of eight items, that is words or pseudowords. All sentence conditions had a consistent syntactic structure (e.g., [[*der Opa*] [*verdarb* [*die Suppe*] [*mit dem Salz*]]]; *the granddad ruined the soup with the salt*). The eight items spanned three phrases connected through the verb. Meaningless sentence conditions were created by keeping function words in place while replacing content words with pseudowords (e.g., [[*der Apo*] [*verworb [die Junne*] [*mit dem Sohr*]]]; *the apo verworbed the junne with the sohr*). Pseudowords were generated based on the real content words using Wuggy (Keuleers & Brysbaert, 2010), matching the original words in syllable length and syllable transition frequency. Each content word and pseudoword was unique across the whole stimulus set. List conditions were created by permuting all items of each sentence, keeping the lexical information equal across real word conditions (e.g., real word list: *der dem Suppe mit Opa Salz die verdarb*; *the the soup with granddad salt the ruined*). Permutation patterns were identical across the real word and pseudoword conditions (e.g., pseudoword list: *der dem Junne mit Apo Sohr die verworb*; *the the junne with apo sohr the verworbed*). To avoid syntactic phrase formation, a number of permutation patterns were excluded (verb-noun, verb-determiner, noun-verb, and verb-preposition; cf. Brennan et al., 2012). This reduced opportunities for syntactic chunking in list conditions. However, due to the flexible word order in German, less common partial phrases were inevitable (e.g., *die verdarb* could, in another context, also be part of a relative clause). Nevertheless, list conditions constituted a stark contrast to the sentence conditions in terms of the availability of syntactic regularities used for syntactic chunking. To avoid encoding differences introduced by the stimulus onset across conditions, the first item was always a lower-case determiner.

Table 4.2: Experiment 1, example of stimulus material: meaningful sentences (Structure+, Meaning+), meaningful word lists (Structure−, Meaning−).

		Structure	
		Sentences	Lists
Meaning	Real words	der Opa verdarb die Suppe mit dem Salz *the granddad ruined the soup with the salt*	die dem Suppe mit Opa Salz die verdarb the the soup with granddad salt the ruined
	Psuedo-words	der Apo verworb die Junne mit dem Sohr *the Apo verworb the Junne with the Sohr*	der dem Junne mit Apo Sohr die verworb *the the Junne with Apo Sohr the verworb*

The permutation of real word sentences into real word lists aimed at dissolving information provided by the syntactic structure, while preserving the lexical meaning. Yet, the permutation could have induced a confound to our manipulation of lexical meaning. That is because each incoming word adds to the amount of lexical-semantic information of the current context, in both real word sentences and lists. We controlled for any differences in the amount of lexical-semantic information provided by the context, between real word sentences and lists, by employing the lexical surprisal metric (e.g., Hale, 2001), a computational measure of a word's unexpectedness given a current context. Specifically, differences in surprisal between real word sentences and lists were minimized to an absolute z-transformed surprisal value smaller than 2.

To this end, a freely available lexicalized top-down left-corner parser (Roark, Bachrach, Cardenas, & Pallier, 2009), trained on the TIGER Treebank (Brants et al., 2004), was employed. To control for effects of animacy (Bonin, Gelin, & Bugaiska, 2014), half of the subjects were animate, half inanimate. To account for possible differences in lexical access demands, word length (i.e., syllable count = 1–3 syllables per word; Spoehr & Smith, 1973) and word frequency (i.e., frequency class = 8–15; Goldhahn, Eckart, & Quasthoff, 2012; Halgren et al., 2002) were constrained in range across items to control for variability. According to these criteria, 96 sequences in the 4 conditions were created, resulting in a total pool of 384 stimuli.

Participants' ability to use syntactic chunking and semantic information to facilitate vWM-intensive sentence processing was evaluated via a serial order task (Bonhage et al., 2014; Bonhage et al., 2017): After each stimulus, participants were asked to judge whether the order of two items from the last stimulus matched the order of presentation. For example, after the stimulus *der Opa verdarb die Suppe mit dem Salz*, the participants may have been asked: *Did the word Opa come before the word mit*? (abbreviated on screen as *Opa <<< mit*). Probing the serial order position emphasized the decoding of syntactic regularities and semantic relations during sentence processing. A total of eight different questions were created for each stimulus, querying any pair of items that were divided by three other items. The prompted words were always selected from different phrases in sentence conditions, assuring similar retrieval difficulty compared to list conditions (Johnson, 1978). For half of those questions, the correct answer was yes, for the other half no. The assignment of questions resulted in a total of 3,072 stimulus–question combinations.

The total set of stimulus–question combinations was distributed across 16 stimulus lists of 192 stimuli each; thus, each stimulus list contained always two conditions (one real word condition, one pseudoword condition) out of one set of the four conditions. The question assignment was counterbalanced within lists across sequences and across sequences across lists. Additionally, the sequences of each stimulus list were pseudo-randomized such that no condition, question, answer type or animate subject occurred consecutively more than four to five times and such that the two conditions of the same stimulus were always separated by at least twenty other sequences.

Procedure

Before the experiment, participants were informed about the four experimental conditions and the task. Stimuli were presented visually, item by item, for 600 ms per item, in white, non-serif letters (Arial, font size 30 pt) in the center of the screen (Sony®, Trinitron, 17 inch, 60 Hz refresh rate) on a gray background. The stimulus presentation was followed by a fixation cross of 2500 ms, followed by a question probing serial order position. Participants had a time limit of eight seconds to answer the question with either yes or no by pressing either of two buttons on a button box. Button assignment was counterbalanced across participants. After the response, participants were provided with visual feedback (happy or sad emoticon) for 400 ms. An inter-trial interval of 2500 ms followed each trial. A practice session of eight trials familiarized participants with the procedure. At five equally distributed points across the experiment, participants could take a break of a maximum of 4 minutes.

Statistical analysis

For statistical analyses, d-prime (d') scores were calculated from participants' yes and no responses to the yes–correct and no–correct questions; after reaction time (RT) outliers (i.e., RTs outside the range of the median RT +/− 2.5 median absolute deviations (MAD); Leys, Ley, Klein, Bernard, & Licata, 2013) and missing responses were removed (both constituted on average 1.68% per participant, SD = 1.66 %). D-prime scores account for participants' inherent response bias (Macmillan & Creelman, 2005) and are computed by subtracting the z-transformed false alarm rate (FA; i.e., yes responses to no–correct questions) from the z-transformed hit rate (H; i.e., yes-responses to yes–correct questions). H and FA of 0 were corrected by 1/(N+1), while H and FA of 1 were corrected by (N-1)/N, whereby N is the number of trials (Macmillan & Creelman, 2005). Within each age group, participants who performed below chance (i.e., d' $<$ 0, two older adults) as well as those which constituted group outliers (i.e., d' $>$ 2 SD, one younger adult and the same two older below chance performers) were excluded from further analyses (in total three participants).

D-prime scores were subjected to a three-way analysis of variance (ANOVA), including the within-participants factors sentence structure (sentences versus word lists) and meaning (real words versus pseudowords) and the between-participants factor age group (younger versus older adults). To assess a potential influence of age differences in vWM capacity (Bopp & Verhaeghen, 2005) on d-prime scores, the three additionally acquired memory measures were first z-transformed across both age groups simultaneously and then averaged into one composite score in order to be later included as a between-subjects covariate into an analysis of covariance (ANCOVA). Any interaction effects were broken down with simple effects analysis, controlling for multiple comparisons with Bonferroni correction.

Post-hoc, we dissociated the impact of the availability of syntactic and semantic constraints for chunking from mere effects of syntactic and lexical predictability; in principle, participants' memory retrieval success could depend on the syntactic or lexical probability of a word to occur within a prior sentence. To assess this potential confound, we computed the lexical-semantic and syntactic predictabilities of the word that was to be retrieved for a given trial, using computational-linguistic methodology (for more details on the calculation of these measures, see Meyer & Gumbert, 2018; Roark et al., 2009). For example, for the question *Did the word Opa come before the word mit?*, predictabilities of the word *Opa (granddad)* of the prior sentence *der Opa verdarb die Suppe mit dem Salz (the granddad ruined the soup with the salt)* were computed. This procedure was repeated for all trials of the structured and meaningful condition. For each participant, both accuracy and surprisal values were then averaged across trials within word position. Across word positions, within participants, we then calculated correlations between accuracy and surprisal values, reasoning that if retrieval demands were confounded with predictability, predictability should significantly correlate with accuracy. Across participants, we corrected the test statistics for multiple comparisons using the False Discovery Rate (FDR) procedure.

4.2.2 Results

The three-way ANOVA (sentence structure × meaning × age group) on the d-prime values showed three main effects: sentence structure ($F(1{,}51) = 182.95$, $p = 2.20 \times 10^{-16}$, $\eta^2 = .39$), meaning ($F(1{,}51 = 57.79$, $p = 6.12 \times 10^{-10}$, $\eta^2 = .06$) and age group ($F(1{,}51) = 6.88$, $p = 1.15 \times 10^{-2}$, $\eta^2 = .09$). Figure 4.1 shows an overview of the single subject and group mean (young versus old) d-prime values for each condition (real word sentences, pseudoword sentences, real word lists, and pseudoword lists). Table 4.3 shows an overview of all response types (hit, miss, false alarm and correct rejection rates) for Experiment 1 and 2 across age groups.

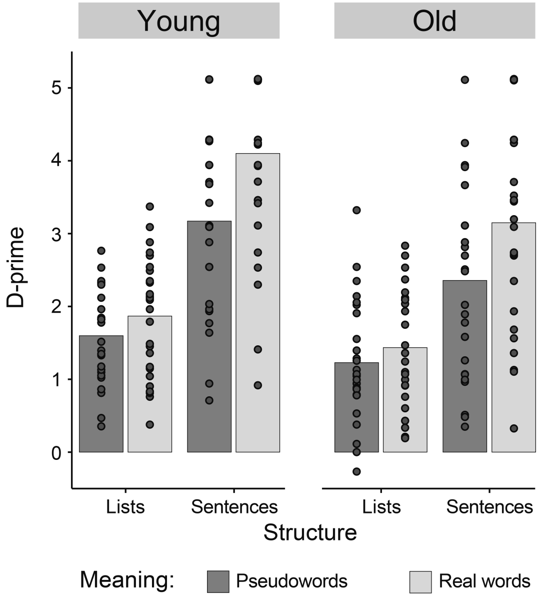

Figure 4.1: Experiment 1, trending age differences in syntactic (sentences versus lists) but not semantic (real words versus pseudowords) processing.

More precisely, performance for sentences (mean = 3.20, *SD* = 1.42) was higher than for lists (mean = 1.54, *SD* = 0.79). Performance for meaningful stimuli (mean = 2.65, *SD* = 1.51) was higher than for meaningless stimuli (mean = 2.10, *SD* = 1.28). Younger adults performed better (mean = 2.69, *SD* = 1.42) than older adults (mean = 2.04, *SD* = 1.35). Furthermore, an interaction effect was found between structure and meaning (F(1,51) = 17.80, $p = 1.00 \times 10^{-4}$, $\eta^2 = .02$). Simple effects analysis (Bonferroni-corrected) showed that while performance was significantly higher for meaningful sentences (mean = 3.64, *SD* = 1.40) than meaningless sentences (mean = 2.77, *SD* = 1.32; $t(102) = –8.33$, $p = 1.55 \times 10^{-12}$), this performance difference was not present for meaningful lists (mean = 1.66, *SD* = 0.82) as compared to meaningless lists (mean = 1.42, *SD* = 0.75; $t(102) = –2.30$, p = 0.09).

Table 4.3: Mean (M) and standard deviation (SD) hit (H), miss (MISS), false alarm (FA) and correct rejection (CR) rates for each condition and age group, summarizing Experiment 1 & 2.

	Young								Old							
	H		MISS		FA		CR		H		MISS		FA		CR	
Experiment 1																
Sentences																
Real words	0.96	0.07	0.04	0.07	0.06	0.10	0.94	0.10	0.89	0.13	0.11	0.13	0.11	0.15	0.89	0.15
Pseudowords	0.91	0.10	0.09	0.10	0.10	0.11	0.90 0.11	0.86	0.13	0.14	0.13	0.20	0.16	0.80	0.16	
Lists																
Real words	0.85	0.09	0.15	0.09	0.26	0.14	0.74	0.14	0.77	0.14	0.23	0.14	0.29	0.15	0.71	0.15
Pseudowords	0.81	0.09	0.19	0.09	0.27	0.15	0.73	0.15	0.77	0.17	0.23	0.17	0.12	0.63	0.12	
Experiment 2																
Sentences																
Real words	0.93	0.08	0.07	0.08	0.12	0.10	0.88	0.10	0.87	0.10	0.13	0.10	0.24	0.11	0.76	0.11
Pseudowords	0.83	0.09	0.17	0.09	0.23	0.15	0.77	0.15	0.74	0.14	0.26	0.14	0.39	0.17	0.61	0.17
Lists																
Real worlds	0.73	0.11	0.27	0.11	0.34	0.16	0.66	0.16	0.74	0.11	0.26	0.11	0.50	0.10	0.50	0.10
Psuedowords	0.73	0.08	0.27	0.08	0.36	0.15	0.64	0.15	0.72	0.11	0.28	0.11	0.51	0.11	0.49	0.11

Moreover, simple effects analysis showed a performance advantage for sentences over word lists, with real words ($t(84) = –13.77$, $p = 1.35 \times 10^{-22}$) and also with pseudowords ($t(84) = –9.42$, $p = 3.50 \times 10^{-14}$), indicating a sentence superiority effect independent of meaningfulness. A direct comparison showed that the advantage of sentence structure was significantly higher within meaningful stimuli (mean d' difference = 1.98, $SD = 1.12$) than within meaningless stimuli (mean d' difference = 1.36, $SD = 0.99$; $t(52) = 8.58$, $p = 1.96 \times 10^{-15}$). No other significant effects were observed (all F < 0.48, all $p > 0.49$) but there was a trending interaction effect between sentence structure and age group (F(1,51) = 3.84, $p = .056$, $\eta^2 = .01$). Simple effects analysis showed that while performance for sentences was significantly higher in younger adults (mean = 3.64, $SD = 1.31$) than older adults (mean = 2.75, $SD = 1.40$; $t(75) = 3.22$, $p = 7.50 \times 10^{-3}$), performance for lists did not differ between younger adults (mean = 1.73, $SD = 0.73$) and older adults (mean = 1.33, $SD = 0.81$; $t(75) = 1.47$, $p = 0.59$). Accordingly, the performance advantage for sentences over lists tended to be larger in younger adults (mean d' difference = 1.77, $SD = 0.79$) than in older adults (mean d' difference = 1.29, $SD = 0.90$; $t(50) = 2.07$, $p = .04$). Yet, as the interaction between age group and sentence structure was only marginally significant, this is not strong evidence for an enlarged sentence superiority effect for younger adults.

The trending interaction effect between age group and sentence structure may have also come about due to age differences in vWM capacity (see Table 4.1). Therefore, the composite score of the vWM measures was included as between-subjects covariate into an ANCOVA. The results showed the same main effects for sentence structure ($F(1,50) = 179.39$, $p = 2.20 \times 10^{-16}$, $\eta^2 = .41$) and meaning ($F(1,50) = 56.67$, $p = 8.98 \times 10^{-10}$, $\eta^2 = .07$) whereas the main effect for age group was not significant anymore. While the interaction effect between sentence structure and meaning ($F(1,50) = 18.12$, $p = 9.01 \times 10^{-5}$, $\eta^2 = .02$) persisted, the trending interaction between age group and structure did not continued to differ significantly from zero. No other effects turned out significant (all $F < 2.31$, all $p > 0.13$), indicating no robust disadvantage for older compared to younger adults despite older adults' vWM limitations.

Finally the additional, post-hoc analysis controlling for predictability effects revealed that neither syntactic (median rho across participants = –0.04, quartile 1 (Q1) = –0.27, quartile 3 (Q3) = 0.10, all FDR-corrected p > 0.99) nor lexical conditional probabilities (median rho across participants = 0.16, Q1 = –0.26, Q3 = 0.30, all FDR-corrected $p > 0.78$) could explain the role of the availability of syntactic and semantic constraints for chunking, respectively.

4.2.3 Discussion

In line with previous studies, Experiment 1 demonstrated an overall lower performance in older adults' sentences processing. We did not observe a specific benefit of available semantic information during sentence processing in the older adults. Moreover, it remains unclear whether the reduced performance could be associated with specific age differences in syntactic processing as only a trending interaction with age group was apparent. We hypothesized that the non-significance of this effect reflects relatively low processing difficulty: Possibly, the reliance on syntactic constraints as an encoding strategy to circumvent capacity limits may only become evident when sentence processing is even more capacity-demanding. Therefore, in Experiment 2, the length of the original eight-item stimuli was increased by three items.

4.3 Experiment 2

The overarching aim of Experiment 2 was to further increase the sensitivity in dissociating the respective contributions of syntactic and semantic constraints to age differences in vWM-intensive sentence processing. To this end, vWM demands were increased by increasing the sequence length from eight to eleven items. Additionally inter-individual vWM capacity differences were assessed to further dissociate language-specific from domain-general constraints of sentence processing.

4.3.1 Methods

Participants

Participant recruitment followed that of Experiment 1 in all aspects, that is, health, handedness, education, consent, and approval of conduction. From a total of 56 participants, after outlier removal (see Experiment 2 – Statistical analysis), the sample consisted of 26 younger (13 males, age range = 20 – 32 years, mean age = 25.12 years, *SD* age = 3.24 years) and 27 older adults (13 males, age range = 60 – 70 years, mean age = 64.19 years, *SD* age = 2.76 years).

Verbal Working Memory Measures

As for Experiment 1, all participants underwent the same short-term memory and vWM measures in the same order (Table 4.1). The scores were then combined into a composite score ($\alpha = 0.73$; see Experiment 1 – Statistical analysis).

Stimuli

The experimental design of Experiment 2 resembles the design of Experiment 1 (Table 4.4). However, to increase participants' reliance on sentence structure and meaning to reduce their overall memory load, the stimulus length was increased to eleven items by adding one phrase of three additional words or pseudowords (e.g., real word sentence: *der Opa verdarb die Suppe mit dem Salz trotz des Rezepts*; the granddad ruined *the soup with the salt despite the recipe*; e.g., pseudoword sentence: *der Apo verworb die Junne mit dem Sohr trotz des Rezerms*; *the apo verworbed the junne with the sohr despite the rezerms*; added phrase underlined). Due to the increased number of items, the permutation patterns of the list conditions were created anew, excluding verb-noun, verb-determiner, verb-determiner-noun, noun-verb, verb-noun-preposition, noun-preposition-noun, and preposition-noun-noun (cf. Brennan et al., 2012). All other criteria were reapplied. In addition, we also controlled for differences in the variability of the sentence length (i.e., the total syllable count of all words) between Experiment 1 and 2 ($F(95,83) = 0.72$, $p = .11$).

The experimental task design was the same as in Experiment 1. However, querying any two items that were divided by three other items in eleven-item sequences increased the set of questions to 14. Therefore, to balance the stimulus–question assignment, a subset of 84 sequences in all 4 conditions were selected from Experiment 1 (i.e., 336 stimuli in total). This created a total of 4704 stimulus–question combinations which were distributed across 28 stimulus lists with 168 stimuli each. Other randomization criteria from Experiment 1 were reapplied with the only difference being the consecutive occurrences of stimulus features which were increased to five to seven times. Also, the two conditions of the same stimulus were separated by at least five other sequences.

Table 4.4: Experiment 2, example of stimulus material: meaningful sentences (Structure+, Meaning+), meaningful word lists (Structure−, Meaning−).

		Structure	
		Sentences	Lists
Meaning	Real words	der Opa verdarb die Suppe mit dem Salz trotz des Rezepts *the granddad ruined the soup with the salt despite the recipe*	der verdarb des mit Suppe dem trotz Salz die Opa Rezepts *the ruined the with soup the despite salt the granddad recipe*
	Psuedowords	der Apo verworb die Junne mit dem Sohr trotz des Rezerns *the Apo verworb the Junne with the Sohr despite the Rezerns*	der verworb des mit Junne dem trotz Sohr die Apo Rezerns *the verworb the with Junne the despite Sohr the Apo Rezerns*

Procedure

The procedure of Experiment 2 was identical to that of Experiment 1.

Statistical analysis

The behavioral measures as well as the statistical analyses in Experiment 2 were identical to those of Experiment 1. In Experiment 2, two younger and one older participant were removed as group outliers (i.e., d′ $>$ 2 SD; there were no below chance performers). Furthermore, reaction time outliers (for detection criteria, see Experiment 1 – Statistical analysis) and missing responses constituted on average 1.60% (SD = 1.6%) per participant.

4.3.2 Results and Discussion

Similar to the results of Experiment 1, the three-way ANOVA (sentence structure × meaning ×age group) showed three main effects: sentence structure (F(1,51) = 181.42, p = 2.20×10^{-16}, $\eta^2 = .41$), meaning ($F(1{,}51) = 62.66$, $p = 1.97 \times 10^{-10}$, $\eta^2 = .15$) and age group ($F(1{,}51) = 22.69$, $p = 1.62 \times 10^{-5}$, $\eta^2 = .19$). Figure 4.2 shows an overview of the single subject and group mean (young versus old) d-prime values for each condition (real word sentences, pseudoword sentences, real word lists, and pseudoword lists).

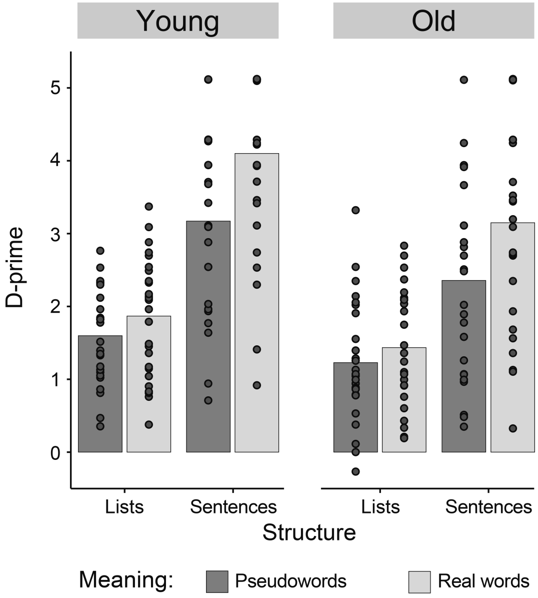

Figure 4.2: Experiment 2, significant age differences in syntactic (sentences versus lists) but not semantic (real words versus pseudowords) processing.

More precisely, performance for sentences (mean = 2.02, *SD* = 1.12) was higher than for lists (mean = 0.85, *SD* = 0.57). Performance for meaningful stimuli (mean = 1.73, *SD* = 1.19) was higher than for meaningless stimuli (mean = 1.14, *SD* = 0.83). Younger adults performed higher (mean = 1.78, *SD* = 1.13) than older adults (mean = 1.09, *SD* = 0.88). Also, an interaction effect was found between sentence structure and meaning ($F(1{,}51) = 45.29$, $p = 1.46 \times 10^{-8}$, $\eta^2 = .11$). A simple effects analysis (Bonferroni-corrected) showed that while performance was significantly higher for meaningful sentences (mean = 2.55, *SD* = 1.03) than for meaningless sentences (mean = 1.48, *SD* = 0.94; $t(102) = –10.36$, $p = 5.11\times 10^{-17}$), this performance difference was not present for meaningful lists (mean = 0.90, *SD* = 0.62) as compared to meaningless lists (mean = 0.80, *SD* = 0.51; $t(102) = –0.95$, $p = 1.00$). Moreover, it showed a performance advantage for sentences over word lists, with real words ($t(99) = –14.65$, $p = 6.43 \times 10–26$) and also with pseudowords ($t(99) = –6.03$, $p = 1.14 \times 10^{-7}$), indicating a sentence superiority effect independent of meaning. A direct comparison corroborated the suggested larger sentence superiority effect for meaningful (mean d’ difference = 1.66, *SD* = 0.85) compared to meaningless stimuli (mean d′ difference = 0.68, *SD* = 0.87; $t(52) = 6.78$, $p = 1.11 \times 10^{-8}$). In contrast, to Experiment 1, the interaction between sentence structure and age group was clearly significant ($F(1{,}51) = 9.88$, $p = 2.79 \times 10^{-3}$, $\eta^2 = .04$). Simple effects analysis showed that while performance for sentences was significantly better for younger adults (mean = 2.51, *SD* = 1.06) than older adults (mean = 1.54, *SD* = 0.98; $t(84) = 5.70$, p = 6.93×10^{-7}), performance for lists did not differ between younger adults (mean = 1.06, *SD* = 0.65) and older adults (mean = 0.65, *SD* = 0.45; $t(84) = 2.46$, $p = 0.06$). Additionally, it was found that both age groups showed a performance advantage of sentences over lists (young: $t(51) = 11.64$, $p = 2.29 \times 10^{-15}$; old: $t(51) = 7.37$, $p = 5.63 \times 10^{-9}$). However, the performance advantage for sentences over word lists was larger in younger (mean d’ difference = 1.27, *SD* = 0.62) than in older adults (mean d′ difference = 0.82, *SD* = 0.63; $t(51) = 2.65$, $p = .01$). No other effects were significant (all $F < 0.43$, all $p > 0.51$).

To assess individual differences, particularly across age groups, we included the vWM composite score as between-subjects covariate into an ANCOVA (for an overview of vWM measures see Table 4.1). The results revealed the same main effects for structure ($F(1{,}50) = 188.44$, $p = 2.20 \times 10^{-16}$, $\eta^2 = .43$), meaning ($F(1{,}50) = 63.57$, $p = 1.83 \times 10^{-10}$, $\eta^2 = .07$) and age group ($F(1{,}50) = 12.57$, $p = 8.61 \times 10–3$, $\eta^2 = .11$) as well as the same interaction effect between structure and meaning ($F(1{,}50) = 46.87$, $p = 1.05 \times 10^{-8}$, $\eta^2 = .12$). However, the effect size of the interaction between age group and structure was reduced ($F(1{,}50) = 5.01$, $p = .03$, $\eta^2 = .02$); yet, the interaction remained statistically significant, indicating a small disadvantage in sentence processing for older compared to younger adults. Remarkably, this age difference goes beyond the domain-general cognitive abilities as indexed by the present set of tasks. No other effects were significant (all $F > 2.58$, all $p < 0.11$). Finally the additional, post-hoc analysis assessing predictability effects revealed that neither syntactic (median rho across participants = 0.09, Q1 = –0.13, Q3 = 0.25, all FDR-corrected $p > 0.76$) nor lexical probabilities (median rho across participants = 0.10, Q1 = –0.14, Q3 = 0.29, all FDR-corrected $p > 0.77$) could explain the role of the availability of syntactic and semantic constraints for chunking, respectively.

4.4 General Discussion

Our study reveals age differences in the use of syntactic and semantic constraints for chunking during sentence processing to reduce vWM demands. The results indicate that the availability of syntactic constraints, which enables syntactic chunking (Bonhage et al., 2017; Zaccarella, Meyer, Makuuchi, & Friederici, 2017), is somewhat less beneficial for older than younger adults (e.g., Feier & Gerstman, 1980; Kemper, 1987; Obler et al., 1991; Stine-Morrow, Ryan, & Leonard, 2000)—particularly when sentences are longer (Experiment 2) but not when sentences are shorter (Experiment 1). Moreover, this age difference persisted even when vWM capacity was accounted for: older adults displayed a disadvantage in the processing of longer sentences. This indicates difficulties in domain-specific beyond domain-general cognitive abilities. In comparison, we did not find any evidence for an increased recruitment of semantic information in older compared to younger adults. Hence, the benefit of the availability of semantic constraints was comparable across age. Moreover, both age groups showed an advantage of processing meaningful over meaningless sentences, but not lists—increasing the sentence superiority effect by meaningful relations between real words for both age groups.

In general, it is clear that allocating resources to the decoding of syntactic regularities in order to chunk sentences reduces vWM costs—also in the aging population (as indicated by Wingfield, Tun, & Rosen, 1995). Our results, however, suggest that the chunking benefit is reduced in older adults, reflected by a lower benefit of the availability of syntactic regularities when vWM demands are high (Experiment 2). More precisely, only sentences where syntactic regularities were present, but not word lists where syntactic regularities were absent, were remembered less by older than younger adults, suggesting age differences in the sentence superiority effect, in particular in the use of syntactic constraints (as supported by another line of research Craik & Masani, 1967; Gilchrist et al., 2008). This effect was present in spite of a potential emphasis of our serial order task on the memory for word order—and thereby syntactic rather than semantic constraints. While such emphasis could have biased the results towards better syntactic memory, our results suggest that this was apparently not the case. Age differences in syntactic processing persist even when a task focuses on the processing of syntactic constraints (e.g., Gao, Levinthal, & Stine-Morrow, 2012; Stine-Morrow et al., 2010). Therefore, regardless of task-related processes, our results suggest that older adults do not benefit as much as younger adults from syntactic constraints to attenuate their vWM limitations during sentence processing.

Contributing to an ongoing debate, our results show age differences in syntactic processing (e.g., Just & Carpenter, 1992; Kemper, 1986, 1987; Obler et al., 1991; Radvansky et al., 2001; Stine-Morrow et al., 2000), contrary to studies suggesting age preservation (e.g., Campbell et al., 2016; Caplan & Waters, 1999; Davis, Zhuang, Wright, & Tyler, 2014; Samu et al., 2017; Tyler et al., 2010). According to the latter studies, older adults use syntactic structure for interpretive processing, despite age-related decrements in vWM capacity (Caplan & Waters, 2013; Caplan & Waters, 1999). However, unlike our study, those studies were restricted to semantically meaningful sentences. Thus, age differences in syntactic processing may have been attenuated or masked by semantic processes, which are known to be more stable across the life span (e.g., Laver, 2009). Yet, further research is needed to better understand these differences in results.

There are multiple potential explanations for a disadvantage in the use of syntactic constraints for chunking at old age. The most plausible explanation, for us, is that when processing demands increase, older adults allocate fewer resources to the decoding of syntactic regularities (Stine-Morrow et al., 1996); that is, their surface form representations fade away more quickly (e.g., Radvansky et al., 2001). As a consequence, older adults may process sentences in a "good-enough" manner (Amichetti et al., 2016; Christianson et al., 2006; Ferreira, 2003; Traxler, 2014), focusing on the situation, thereby extracting gist rather than detailed knowledge (Tun, Wingfield, Rosen, & Blanchard, 1998). Age differences in the reliance on this processing heuristic appears to persist even when the task context puts particular emphasis on enriched sentence processing (Stine-Morrow et al., 2010), as was the case for the serial order judgment in the present study. Good-enough sentence processing has been proposed to lead to incomplete and shallow representations of syntactic and semantic information (Ferreira & Patson, 2007). The depth to which these representations are processed is associated with the degree of cognitive analysis: higher levels of processing create stronger memory traces (Craik & Lockhart, 1972; Craik & Tulving, 1975). Hence, it is possible that the disadvantage in using syntactic constraints for chunking may arise because good-enough sentence processing leads to shallow representations of syntactic regularities which constitute the basis for the chunking mechanism. If fewer resources are allocated to syntactic regularities, thereby creating good-enough rather than detailed syntactic representations, the binding process may become deficient. To this end, binding may be understood as the core basis of chunking: single elements can be bound into chunks through their strong associations with each other. In support of this hypothesis, it is well known that older adults are generally deficient in binding information to larger entities (Chalfonte & Johnson, 1996; Fandakova, Sander, Werkle-Bergner, & Shing, 2014; Mitchell, Johnson, Raye, & D'Esposito, 2000; Sander, Lindenberger, & Werkle-Bergner, 2012; Sander, Werkle-Bergner, & Lindenberger, 2011; Shing et al., 2010). Our results showed a smaller processing advantage of sentences over lists in older than younger adults, possibly indicating that good-enough processing of syntactic constraints may be insufficient for proper syntactic chunking.

As an alternative to the good-enough processing hypothesis, it is also possible that the diminished advantage of processing sentences over lists, particularly in the more resource-demanding Experiment 2, resulted from an overload of older adults' vWM capacity associated with increased supraspan interference (Craik & Masani, 1967; Melton, 1963; Wingfield et al., 1995). During sentence processing, supraspan interference can occur when capacity limits are exceeded and syntactic features start to interfere with each other. The ability to suppress interference is a critical determinant of successful sentence comprehension (Glaser, Martin, Van Dyke, Hamilton, & Tan, 2013; Lewis et al., 2006; Santi, Friederici, Makuuchi, & Grodzinsky, 2015; Van Dyke, 2007). Gilchrist et al. (2008) observed that recall performance declined in older adults with increasing number of chunks, particularly so in longer compared to shorter sentences. Similarly, in our study, older adults' performance was particularly compromised relative to younger adults when sentences were longer (Experiment 2). Therefore, reduced vWM capacity in older compared to younger adults may be associated with increased supraspan interference during sentence processing (Craik & Masani, 1967; Hasher & Zacks, 1988). However, our results do not support this theory given that vWM capacity differences alone cannot explain the age differences in syntactic chunking: when age-related differences in vWM capacity were accounted for, older adults' disadvantage in syntactic chunking remained considerable. Nonetheless, supraspan interference may not only be subject to vWM capacity limitations but also to age-related differences in the general ability to inhibit interfering material (Hasher & Zacks, 1988). Therefore, future studies should capture the influence of supraspan interference by using additional tasks like the Stroop (Stroop, 1935) or flanker task (Eriksen & Eriksen, 1974).

A third possibility for age differences in the ability to use syntactic constraints for chunking is that older adults may have more difficulties than younger adults in using (syntactic) templates (for an overview of template theory see, Charness, 1981; Gobet & Simon, 1996). Syntactic relationships may be represented as templates, providing structures with fixed slots that have to be filled with variable information (Van Valin & LaPolla, 1997). It is presumed that with experience single elements do not have to be repeatedly chunked into larger entities but at one point can be stored as larger chunks (Gobet & Simon, 1996), like a reoccurring sequence of word categories building a common phrase structure. These common phrase structures may then function as templates. Templates, in general, are thought to be stored in long-term memory (LTM Gobet & Simon, 1996; Guida, Gobet, Tardieu, & Nicolas, 2012). With syntactic processing being rather automatic, syntactic templates may constitute an implicit, procedural-like long-term memory. Both implicit and procedural memories are relatively spared from age-related decline (e.g., Mitchell, Brown, & Murphy, 1990). Moreover, in our study, we used the same syntactic structure for all sentences. Therefore, a disadvantage in the use of syntactic regularities for chunking is most likely not associated with difficulties in using (the same) syntactic templates (over and over again). However, further research is needed to examine the various options and tackle the specificities of the disadvantage in syntactic chunking. While the results showed that older adults do not benefit from syntactic constraints as much as younger adults, older adults showed a similar advantage in the use of semantic information when available. That is, younger and older adults both remembered meaningful words better than meaningless pseudowords. This may seem contrary to prior findings showing that older adults have greater difficulties than younger adults in recoding meaningful compared to meaningless words (e.g„ Heron & Craik, 1964). However, our findings additionally show that the advantage in the use of available semantic information was increased in the presence of syntactic constraints. That is, both age groups took advantage of the semantic information of words, in particular when the words were also syntactically related. Therefore, our findings may relate to an enrichment of lexical-semantic representations by relational semantics. This result substantiates theories indicating a role of meaningfulness to syntactic chunking (e.g., Tulving & Patkau, 1962) while refuting the position that there is no interaction between sentence structure and meaningfulness (e.g., Epstein, 1962). In light of age differences in syntactic chunking, the intact ability of semantic processing may become relatively more salient for sentence processing at old age. Therefore, older adults may change their sentence processing strategy towards a semantic approach ((Amichetti et al., 2016). However, further research is needed to substantiate this suggestion.

4.5 Conclusion

Our study suggests that sentence processing is facilitated by both the ability to use syntactic constraints for chunking and the availability of semantic information. While both younger and older adults profit from semantic information to a similar extent, the benefit of using syntactic constraints for chunking decreases with normal aging. Hence, the relative importance of semantic information processing is increased for successful language comprehension in old age. This finding persisted even when individual differences in vWM capacity were accounted for, pointing to a disadvantage in language-specific b eyond domain-general cognitive abilities in old age. The salience of semantic information may lead to a change in sentence processing strategies towards a semantic approach later in life. Further research endeavors are needed to support this hypothesis.

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Chapter 5

General Discussion

Healthy aging has been shown to affect language processing on both the cognitive and neural level (i.e., neurocognitive level). The current debate on the effects of neurocognitive aging on language processing centers around two diverging findings: the preservation and the decline of language processing in healthy aging (for reviews see Burke & Shafto, 2008; Peelle, 2019; Shafto & Tyler, 2014; Wingfield & Grossman, 2006). In contrast, the present thesis argues for a combination of both: the preservation of semantic processing and the decline of syntactic processing (Beese et al., 2019). Hence, healthy aging differentially affects distinct language-specific processes. Moreover, the work presented in the current thesis also demonstrated detrimental effects of healthy aging on processes that are not specific to language per se but rather support language processing in general, like vWM. That is, a decline in vWM was found to contribute to a general decline in sentence processing in old age. This decline in sentence processing was reflected by alterations of the electrophysiological dynamics underlying vWM in healthy aging (Beese et al., 2017; Beese et al., submitted). These findings provide some specificity to a previously suggested model of sentence processing in old age, the two-component model (Wingfield & Grossman, 2006). The model is comprised of one language-specific and one domain-general processing component. On the basis of this thesis, the language-specific component can be refined to declining syntactic processes and preserved semantic processes. The domain-general component can be refined to limitations in vWM encoding. Therefore, the current thesis advances current models of language processing in healthy aging and, thereby, contributes to the current debate on the effects of neurocognitive aging on language processing.

5.1 Summary of Experimental Findings

The present thesis investigated the effects of language-specific and domain-general neurocognitive aging on sentence processing in three studies. First of all, it was investigated whether older adults' difficulties in sentence comprehension would be predicted by brain-related age differences in the prerequisites for sentence processing. That is when electrophysiological dynamics at rest already differ with increasing adult age. Specifically, age differences in the resting electrophysiological dynamics, related to language processing or associated domain-general cognitive processes, may be associated with older adults' sentence comprehension difficulties. The results revealed two electrophysiological resting-state networks that were spatially and temporally decoupled within the theta frequency range. One network constituted by left dorso-frontal regions predicted sentence comprehension independently of age. The other network comprising frontal midline regions was found to be associated with vWM. The latter predicted older adults' sentence comprehension difficulties. This suggests that an age-related decline in language processing can be associated with the effects of neurocognitive aging on vWM. In order to better understand the role of vWM decline for language processing in healthy aging, a second study was conducted. This study was motivated by the common presumption that accurate sentence comprehension relies on the successful encoding of sentences into vWM. To this end, the effects of healthy aging on the electrophysiological network dynamics underlying sentence encoding were examined. The results revealed that older adults' difficulties in sentence comprehension may indeed be associated with alterations of the electrophysiological network dynamics in the alpha frequency band. Specifically, an inversion from decreased to increased alpha power was observed across the lifespan. With alpha power being commonly linked to inhibition, increased alpha power in old age may indicate that older adults achieve accurate sentence comprehension by inhibiting the encoding of detailed information that would otherwise overload their limited vWM capacity. Thereby, the inhibition of information can serve to extract fewer details and rather focus on the gist information in a top-down manner. These results substantiate the relative importance of domain-general neurocognitive aging for sentence comprehension in healthy aging. However, these adverse effects of domain-general neurocognitive aging on sentence comprehension may be attenuated through language-specific constraints. That is, on the basis of semantic and syntactic constraints, relations between words can be established to reduce the vWM load from individual to relational word information. However, it remained an open question whether younger and older adults differ in the extent to which they exploit semantic and syntactic constraints to reduce the vWM load. The results presented here indicate that syntactic constraints are somewhat less beneficial for older than younger adults, while the benefit of semantic constraints was comparable across age groups. One possible explanation is that older adults do not extract detailed syntactic information, which would allow them to establish syntactic relationships between words, which could in turn reduce the vWM load. This would substantiate the hypothesis that older adults extract fewer details and may instead focus on gist information in a top-down manner. Altogether, the findings of this thesis converge on the detrimental effects of declining domain-general cognitive functions on sentence processing while diverging on the domain-specific cognitive functions into the decline of syntactic processes and preservation of semantic processes.

5.2 A Framework of Neurocognitive Aging – Revisited

Preempting the take home message of this thesis, the findings of this thesis reveal a multifaceted nature of the effects of language-specific and domain-general neurocognitive aging on sentence processing. On the basis of these findings, the framework introduced in Figure 1.1 (Chapter 1.1) can be refined (see Figure 5.1). First, *Cognitive Aging* (the foot of Figure 1.1) can be modified as *Syntactic Aging* as only syntactic but not semantic processes decline in healthy aging. Second, with respect to *Functional Brain Aging*, the functional electrophysiological networks have been found to change in healthy aging both at rest and task. Both alterations were associated with detrimental age effects of vWM on sentence processing. This suggests that in the framework *Cognitive Demands* can be specified as *vWM Demands* and the general (electro-)*Physiological Modulations* can be specified as *Theta and Alpha Band Modulations* (for the specifics see the Summary of the Experimental Findings, 5.1). While this is a first step into a better understanding of the effects of neurocognitive aging on sentence processing, possible future modifications of this framework derive from the discussion in Chapter 5.7.

This framework adds some specificity to the two-component model (Wingfield & Grossman, 2006) according to which the functional integrity of the language network remains preserved, while the functional integrity of an associated domain-general network that supports sentence processing is compromised. However, this model leaves open which exact language processes remain preserved and which exact domain-general processes decline. Adding specificity, the results of this thesis reveal that not all language processes are preserved but that instead healthy aging has some detrimental effects on syntactic processes, while only semantic processes remain preserved (Beese et al., 2019). Moreover, the results of this thesis specify limitations in vWM capacity and encoding as domain-general cognitive functions to

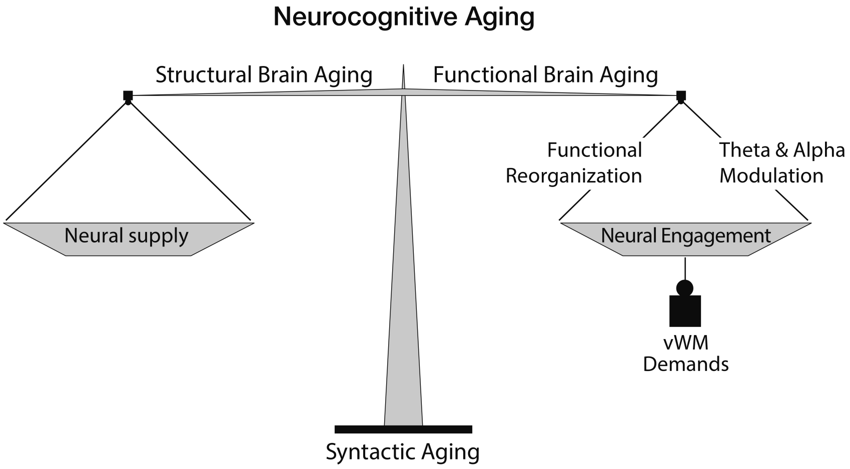

Figure 5.1: A Framework of Neurocognitive Aging – Revisited.

contribute to age-related sentence comprehension difficulties (Beese et al., submitted). The multifaceted nature of language-specific (5.3) and domain-general neurocognitive aging (5.4) that the results of this thesis reveal will be discussed in the following section. Then these findings will be briefly evaluated in terms of the underlying mechanism of functional brain aging (5.5). Subsequently, limitations (5.6) and new research avenues (5.7) will be proposed upon which the framework of neurocognitive aging of sentence processing can be further developed.

5.3 Age-Related Preservation and Decline of Language-Specific Processes

One research objective of this thesis was to investigate the effects of healthy aging on language-specific processes. While previous studies examined either semantic or syntactic processes, in this thesis semantic and syntactic processes were directly compared in one study design by dissociating and isolating these processes from each other. The results point to a combination of an age-related preservation of the use of semantic constraints and an age-related decline in the use of syntactic constraints (Beese et al., 2019). This may indicate a decrease in the relative importance of syntactic constraints for sentence processing in healthy aging. Possibly, older adults extract fewer detailed syntactic information based on which sentence processing could be constrained. At the same time, semantic processing remains preserved in old age which may increase its relative importance for sentence processing in healthy aging. Interestingly, when linking this shift in the relative importance of distinct language-specific processes to the automaticity of those processes, the question arises why such an automatic process as syntactic processing would decline with age. One possible answer to this question points to an association with domain-general cognitive aging. All of these points will be discussed here.

Previous research investigated semantic and syntactic processing in separation and without dissociating or isolating these processes from one another. That is, to date, studies were typically focused on either semantic or syntactic processing by varying the degree to which stimulus materials taxed semantic or syntactic processing demands, respectively (Chapter 1.2.1; Campbell et al., 2016; Peelle et al., 2010; Stine-Morrow et al., 1996; Tyler et al., 2010). However, commonly, stimulus materials consist of sentences that are both syntactically well-formed and semantically meaningful which neither dissociates nor isolates semantic and syntactic processing from each other. This complicates the comparison of the extent to which these processes are affected by healthy aging. For instance, both Peelle et al. (2010) and Tyler et al. (2010) examined the effects of healthy aging on syntactic processing by comparing younger and older adults' comprehension of syntactically-well formed and meaningful sentences that varied in the syntactic processing demands. While Peelle et al. (2010) shows that older adults had more difficulties than younger adults in comprehending syntactically demanding sentences, Tyler et al. (2010) found that older and younger adults' comprehension performance did not differ from each other. These two competing findings illustrate that when stimulus materials do not isolate the process of interest, findings diverge by supporting either an age-related preservation of syntactic processing (e.g., Campbell et al., 2016; Caplan & Waters, 1999; Samu et al., 2017; Shafto & Tyler, 2014; Tyler et al., 2010) or an age-related decline in syntactic processing (e.g., Just & Carpenter, 1992; Kemper, 1986, 1987; Obler et al., 1991; Radvansky et al., 2001; Stine-Morrow, Ryan, & Leonard, 2000). However, this allegedly age-related preservation of syntactic processing may actually be masked by the relative age-related preservation of semantic processing when stimulus materials are constituted by semantically meaningful sentences (e.g., Laver, 2009). In contrast, when semantic and syntactic processes are dissociated and isolated from each other, as in this thesis, syntactic processing appears to decline while semantic processing remains preserved in healthy aging (e.g., Beese et al., 2019). This emphasizes the importance of disentangling different language-specific processes to better understand the effects of healthy aging on sentence processing in the future.

Aiming for a good level of sentence comprehension, older adults may shift their focus from syntactic to semantic information, as contrary to syntactic processing, semantic processing appears to be preserved (e.g., Amichetti, White, & Wingfield, 2016; Beese et al., 2019). This shift in focus may be reflected by a more effective allocation of processing resources in healthy aging (e.g., Bäckman & Dixon, 1992). In light of age-related decline in syntactic processing, older adults have been found to allocate fewer resources to syntactic information (e.g., Stine-Morrow et al., 1996). If older adults allocated fewer resources to the available syntactic information in sentences, older adults may extract fewer syntactic details upon which syntactic relations could be established to constrain sentence processing. This allocation of fewer resources to syntactic information may serve to balance the information load, considering older adults' limited processing resources (e.g., Bopp & Verhaeghen, 2005). That is, older adults may benefit from more controlled, top-down sentence processing to avoid an information overload. This may explain why older adults do not benefit as much as younger adults from the availability of detailed syntactic information in sentences as compared to word lists in this thesis (Beese et al., 2019).

However, in spite of insufficient syntactic details, older adults typically still get the gist of sentences (e.g., Reder, Charney, & Morgan, 1986; Tun, Wingfield, Rosen, & Blanchard, 1998). For instance, older adults judge the plausibility of a story as well as younger adults but have difficulties judging exact details of the story (Reder et al., 1986). This suggests that older adults may just process sentences in a "good-enough" manner (e.g., Amichetti et al., 2016; Christianson, Williams, Zacks, & Ferreira, 2006; Ferreira, 2003; Malyutina & den Ouden, 2016; Traxler, 2014). Such good-enough sentence processing yields sparse and shallow representations (Ferreira & Patson, 2007) whose memory traces are typically weaker due to the shallow depth of processing (e.g., Craik & Lockhart, 1972; Craik & Tulving, 1975). Following this train of thought, if memory traces of syntactic information are weak, they may also decay faster (Sachs, 1967). The decay of syntactic memory traces has been shown to be faster in older than younger adults (e.g., Radvansky et al., 2001), reducing the long-lasting availability of syntactic information for older adults. As syntactic memory traces decay, older adults may have difficulties to establish syntactic relations between words based on detailed syntactic information (e.g., Radvansky et al., 2001; Stine-Morrow et al., 1996; Stine-Morrow, Morrow, & Leno, 2002). This may force older adults to rely on plausibility or gist information rather than on detailed syntactic information relative to younger adults (e.g., Reder et al., 1986; Tun et al., 1998). Therefore, the finding of this thesis that older adults do not benefit from syntactic information suggests that older adults may process in a good-enough manner. Shifting towards good-enough processing may help older adults to better understand what has been said (i.e., the semantics) rather than how it was said (i.e., the syntax), thereby reducing resource demands.

Nevertheless, at first glance, it may be rather astonishing to find a process as automatic as syntactic processing compromised in old age. In particular, older adults' life-long experience with sentence processing and reoccurring sequences of word categories that make up common sentence structures would suggest that also the allocation of resources to such syntactic information should remain subconscious and automatic in healthy aging (e.g., Frazier, Carlson, & Clifton, 2006; Gobet & Simon, 1996; Marslen-Wilson & Tyler, 1975). However, that does not seem to be the case, even when the same sentence structure reoccurs again and again in an experimental setting as in Beese et al. (2019): older adults do not benefit as much as younger adults from the reoccurring word order in sentences over the random word order in word lists. That is, older adults remembered sentence-embedded words less than younger adults which was not the case for words in word lists (as supported by e.g., Craik & Masani, 1967; Gilchrist et al., 2008). One explanation for this finding is that older adults may not benefit as much as younger adults from the enriched syntactic relations between individual words in sentences. This entails that syntactic processing may not only be an automatic skill but also a resource-demanding integration process (e.g., Payne & Stine-Morrow, 2016). That is, part of syntactic processing is the integration of individual words into phrases and sentences based on syntactic information (e.g., Daneman & Carpenter, 1983; Haberlandt, Graesser, Schneider, & Kiely, 1986). Previous studies found that older adults allocate more resources to boundaries between phrases than sentences compared to younger adults (e.g., Stine-Morrow et al., 1996; Stine, 1990). This likely indicates that older adults focus on the integration of words into phrases rather than sentences. Hence, older adults wrap up the integration after phrases which leads them to segment sentences into smaller fragments than younger adults. While this may seem like a good way to reduce the vWM load, phrase-level wrap-ups have been found to be more time-consuming and cognitively effortful (e.g., Payne & Stine-Morrow, 2012, 2014). Therefore, phrase-level wrap-ups increase vWM demands. Considering older adults' vWM limitations, the greater number of wrap-ups at phrase-level boundaries may be related to poorer sentence comprehension in older than younger adults (e.g., Payne & Stine-Morrow, 2012; Stine, 1990). In other words, the allocation of resources to syntactic processing may still be automatic in older adults but seems to be less effective for resource-demanding integration processes. Future studies should discern automatic from resource-demanding processes during syntactic processing in isolation of semantic processing, to better understand where age differences in syntactic processing come from.

In sum, an age-related decline in syntactic processing may be associated with an ineffective allocation of resources which yields insufficient syntactic details (i.e., good-enough representations) to integrate words into phrases and sentences which in turn increases the resource demands of an otherwise automatic process.

5.4 Language Decline Through Age-Related Declines of Domain-General Processes

In addition to the effects of healthy aging on language-specific processes, this thesis also examined the effects of domain-general neurocognitive aging on sentence processing. That is because healthy aging does not just affect language-specific processes but also processes that are not language-specific per se but still support language processing in general. For instance, in the past, limitations in older adults' vWM have been shown to contribute to their difficulties in sentence comprehension (e.g., DeDe & Flax, 2016; Just & Carpenter, 1992; Kemper et al., 2004). The findings of this thesis offer a deeper understanding of the contribution of older adults' limitations in vWM on sentence comprehension. As a brief reminder, on the one hand, older adults' difficulties in sentence comprehension were found to be predicted by alterations of the resting-state network relevant for vWM (Beese et al., 2017, Chapter 2). On the other hand, older adults' difficulties in sentence comprehension were associated with detrimental effects of healthy aging on the encoding of sentences into vWM. This was reflected by age differences in the electrophysiological dynamics underlying sentence encoding (Beese et al., submitted, Chapter 3). However, older adults' vWM limitations did not affect semantic and syntactic processes differently (Beese et al., 2019, Chapter 4). The following discussion will shed some light on the effects of vWM limitations on sentence processing in healthy aging. As a starting point, the specificity of vWM will be discussed as vWM limitations did not differentially affect distinct language-specific processes. Next, poor sentence comprehension in older adults will be related to the deficient encoding of sentences into vWM. As to that, the possibility will be discussed that sentence comprehension difficulties arise in older adults when too much information is encoded. That is, older adults may need to inhibit the encoding of information that would otherwise overload their limited vWM capacity to accurately comprehend sentences. Hence, the inhibition of information yields fewer encoded details and allows older adults to focus on the gist information in a top-down manner.

The effects of healthy aging on vWM were found to compromise sentence processing in general but may not differentially contribute to age differences in syntactic and semantic processing (Beese et al., 2019). At a first glance, this finding may not be surprising as resource-demanding integration processes occur on both the syntactic and the semantic level. Nevertheless, Beese et al. (2019) observed that older adults do not benefit from the use of syntactic constraints as much as younger adults, while the benefit of semantic constraints was comparable across age groups. This in turn would suggest that resource limitations in vWM specifically compromise syntactic processing. As this was not observed by Beese et al. (2019), it is possible that the generalization of working memory capacity to anything that is verbal does not capture the linguistic diversity of sentence processing. Instead, it raises the question whether vWM resources can be disentangled into semantic and syntactic aspects as previous clinical work suggested (e.g., Martin, 1987; Martin & He, 2004; Martin & Romani, 1994; Martin, Shelton, & Yaffee, 1994). This view is challenged by one line of research which proposes that sentence processing is constrained by one vWM resource (single-resource theory, Just & Carpenter, 1992). This resource is equally taxed by distinct language-specific processes as well as the overall amount of verbal information. Accordingly, older adults' sentence comprehension difficulties would be associated with limitations in this one vWM resource (Just & Carpenter, 1992). In contrast, according to another line of research, there are separate resources for language-specific processes as well as the overall verbal load (separate-sentence-interpretation-resource theory, Caplan & Waters, 1999). Accordingly, older adults' sentence comprehension difficulties could be associated with limitations in more specific syntactic aspects of working memory resources (Caplan & Waters, 1999; Waters & Caplan, 1996a, 1996b, 2001, 2002). However, more research is needed to experimentally dissociate semantic and syntactic aspects of working memory in order to associate those with age-related sentence comprehension difficulties more directly.

Age-related sentence comprehension difficulties may further be associated with limitations in the encoding of sentences into vWM. As sentences unfold, each piece of upcoming verbal information is encoded into vWM. In this process, information that is just being encoded may interfere with the already encoded information (e.g., Lewis, Vasishth, & Van Dyke, 2006). Encoding interference has been shown to play a crucial role for sentence processing, as reflected in increased processing times (e.g., Gordon, Hendrick, & Levine, 2002; Lewis & Vasishth, 2005; Lewis et al., 2006). In particular in Beese et al. (2017) and Beese et al. (submitted), participants had to encode sentences of six nouns that were similar with respect to both syntactic (gender and syntactic category information) and semantic information (six person words, often of one semantic category). For instance, a sentence about sports may have consisted of three female and three male person words each referring to some type of athlete. In this case, syntactic and semantic similarities may have increased the degree to which the encoding of new information interfered with already encoded information as sentences unfolded. This would increase the processing load which may in turn overload older adults' limited vWM capacity (e.g., Craik & Masani, 1967; Melton, 1963; Wingfield, Tun, & Rosen, 1995). Therefore, the ability to inhibit interference is a critical determinant of successful sentence comprehension (e.g., Glaser, Martin, Van Dyke, Hamilton, & Tan, 2013; Lewis et al., 2006; Santi, Friederici, Makuuchi, & Grodzinsky, 2015; Van Dyke & McElree, 2006). While interference might offer an explanation for the results of Beese et al. (2017) and Beese et al. (submitted), it does not explain why only syntactic processing would be affected by healthy aging (Beese et al., 2019). One speculative explanation is that syntactic information is easier interfered with than semantic information. That may be because syntactic processing leads to less memorable, shallow encoded memory traces while semantic processing yields highly memorable, deeply encoded memory traces (e.g., Bobrow & Bower, 1969; Craik & Lockhart, 1972; Craik & Tulving, 1975; Jacoby, Craik, & Begg, 1979; Kamp & Zimmer, 2015; Rosenberg & Schiller, 1971; Schulman, 1971; Treisman & Tuxworth, 1974). Hence, the encoding of syntactic information may yield shallow memory traces that may be less distinctive and can therefore be easily interfered with by already encoded information. However, as this explanation is highly speculative at this point, future studies need to follow up on examining the effects of healthy aging on the interaction between interference and depth of processing during sentence processing.

As a critical determinant of successful sentence comprehension, the ability to inhibit interfering information has been found to be more easily compromised in old age (e.g., Gazzaley et al., 2008; Hasher & Zacks, 1988; Oberauer & Kliegl, 2010; Pelegrina, Borella, Carretti, & Lechuga, 2012; Radvansky et al., 2001; Rodriguez-Villagra, Gothe, Oberauer, & Kliegl, 2013; Stoltzfus, Hasher, & Zacks, 1996). That is, for instance, when the amount of information in sentences increases, older adults have more difficulties to inhibit less important information than younger adults and instead focus on the more important information (e.g., Stine & Wingfield, 1988). Such deficient inhibition likely increases the amount of information that is encoded into vWM which may overload older adults' limited vWM capacity (e.g., Eriksen & Eriksen, 1974; Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Vogel, McCollough, & Machizawa, 2005; Zanto & Gazzaley, 2009). For instance, contrary to younger adults, older adults appear to keep alternative text interpretations in vWM which increases the amount of competing information held in vWM (Hamm & Hasher, 1992). Such age-related inhibitory deficits were previously related to older adults' sentence comprehension difficulties (e.g., Carlson, Hasher, Zacks, & Connelly, 1995; Connelly, Hasher, & Zacks, 1991; Hamm & Hasher, 1992; Taler, Aaron, Steinmetz, & Pisoni, 2010). Therefore, inhibitory deficits may offer an explanation for the findings in Beese et al. (submitted) which revealed age differences in the electrophysiological dynamics (in particular, alpha power) that have previously been associated with inhibition (e.g., Jensen & Mazaheri, 2010). As an index of inhibition, alpha power increased in older adults during the encoding of later correctly comprehended sentences compared to the encoding of later incorrectly comprehended. On this basis, the hypothesis arose whether older adults would extract less information by inhibiting the encoding of information that is not required to get the gist of sentences and that would otherwise overload their vWM capacity. However, this hypothesis remains to be tested more directly by future research.

An extraction of less information by inhibiting the encoding of information, that would otherwise overload older adults' limited vWM capacity, may also suggest that older adults process sentences in a more controlled, top-down manner. Top-down processing entails the inhibition of less important information (e.g., Watson & Humphreys, 1997) while focusing on the detection of target features (e.g., Müller, Heller, & Ziegler, 1995; Wolfe, 1994). Top-down processing has not only been granted an increased importance in old age (e.g., Madden & Allen, 1991) but previous studies have also suggested that older adults rely more on top-down than bottom-up processing (e.g., Whiting, Madden, & Babcock, 2007; Zanto & Gazzaley, 2009). In fact, older adults have been shown deficient in bottom-up processing (e.g., Madden, 2007; Madden, Whiting, & Huettel, 2005; Wingfield, Aberdeen, & Stine, 1991). That is, healthy aging has been associated with a decrease in bottom-up processing (e.g., Madden & Allen, 1991; McAvinue et al., 2012; Schneider & Pichora-Fuller, 2000), whereas top-down processing remains preserved in old age (e.g., Madden, Whiting, Cabeza, & Huettel, 2004; Whiting, Madden, Pierce, & Allen, 2005). This shift in the relative importance from bottom-up to top-down processing across the lifespan has been shown to play a role in discourse processing (e.g., Marslen-Wilson & Tyler, 1980; McClelland, 1987). That is, older adults benefit more from top-down, contextually-driven information processing while younger adults use a data-driven, bottom-up approach (e.g., Stine-Morrow et al., 1996). Linking these previous findings to the results of Beese et al. (submitted), older adults may inhibit the extraction of rich and detailed information and instead encode sentences in a top-down manner (e.g., Whiting et al., 2007; Whiting, Sample, & Hagan, 2014; Wingfield et al., 1991) that is good-enough to extract the gist of sentences (e.g., Christianson et al., 2006; Ferreira & Patson, 2007; Tun et al., 1998). This in turn may entail that older adults inhibit the encoding of syntactic details, offering an explanation why older adults' use of syntactic constraints was deficient (Beese et al., 2019). While these links between good-enough processing, inhibition and top-down processing are quite speculative at this point in time, the possibility thereof should be more directly examined by future research.

5.5 Mechanisms of Functional Brain Aging in Sentence Processing

Electrophysiological networks that are relevant for sentence processing have been found altered in healthy aging. Such alterations reflect functional brain aging and may be linked to the common mechanisms of functional brain aging: neural dedifferentiation and compensation. Neural dedifferentiation is indexed by alterations in the electrophysiological networks that do not lead to the maintenance of youth-like performance levels (e.g., Baltes & Lindenberger, 1997). In this vein, in Beese et al. (2017), the electrophysiological modulation of the resting-state network did not yield maintained youth-like performance in older adults. Instead, older adults were found to have difficulties comprehending sentences. These difficulties were associated with the modulation of an electrophysiological network outside the core language network. Hence, the electrophysiological networks engaged during sentence processing differed between younger and older adults. In contrast, in Beese et al. (submitted), the electrophysiological modulation of the task-related network illustrated that older adults down-regulate posterior regions and up-regulate anterior regions of the same network activated by younger adults. Such modulation is in line with the well established finding of posterior-to-anterior shifts in aging (PASA ; e.g., Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Grady, 2012; Park & Rugg, 2008). According to PASA, anterior regions such as the prefrontal cortex are increasingly recruited while posterior regions such as the parietal cortex become decreasingly recruited. Task performance has been suggested to rely on strategies engaging parietal regions in younger adults while the same task performance may be maintained in older adults by relying on strategies involving frontal regions (McEvoy, Pellouchoud, Smith, & Gevins, 2001). However, the fact that older adults could not maintain youth-like performance in Beese et al. (submitted) raises the possibility of an alternative mechanism at work. That is, older adults may have attempted to respond to increasing cognitive demands by compensating for reduced neural resources, but may have employed an inefficient processing heuristics (e.g., Cabeza & Dennis, 2012). Attempted compensation occurs when neural systems cannot compensate for reduced neural resources due to the amount of cognitive demands posed by the task at hand (see compensation-related utilization of neural circuits hypothesis, CRUNCH, 1.3.2). In light of the results of Beese et al. (submitted), neither compensation nor neural dedifferentiation can indistinguishable be supported, as the task demands were always high and always yielded poor sentence comprehension in older adults. In contrast, if task demands had been low and both neural and behavioral responses differed, the results could be clearly interpreted as neural dedifferentiation as there may not have been anything to compensate for. Moreover, successful compensation can only be supported when differential age-related neural responses have a positive effect on cognitive performance. Future studies may vary the cognitive demands posed by the stimulus material and task to tease apart different mechanisms (i.e., neural dedifferentiation from compensation) that may support sentence processing in old age.

5.6 Limitations

While a lot of care went into designing the tasks used in this thesis, some limitations should be raised with respect to the nature of task designs in experimental aging research. First, the nature of experimental research often entails a task-based assessment of the process of interest. Thereby, inter-individual differences in task-related cognitive functions may confound inter-individual differences in the process of interest. Hence, age differences in sentence processing, as revealed in this thesis, may have emerged in response to the effects of healthy aging on task-related cognitive functions that are not language-specific but still support language processing in general. That is usually the case when tasks probe the presented information after sentences have already been processed in full. In these cases, all encoded information has to be maintained in vWM until the probe is presented (e.g., Campbell et al., 2016; Wingfield & Grossman, 2006). These types of post-stimulus, offline tasks likely increase domain-general cognitive processing demands such as vWM demands (e.g., Campbell & Tyler, 2018). Therefore, studies that use offline tasks may find age differences in sentence processing confounded by older adults' limitations in vWM. For that reason, inter-individual differences in vWM capacity were taken into account in all three studies presented in this thesis which used offline tasks. While the results of two of these studies showed that older adults' sentence comprehension difficulties were contributed by vWM limitations (Beese et al., 2017; Beese et al., submitted), vWM limitations had no impact on the age differences in sentence processing in Beese et al. (2019). Yet, again other studies show that age differences in sentence processing disappear once inter-individual differences in vWM capacity are taken into account (e.g., DeCaro et al., 2016). The fact that these findings are so different suggests that it is not clear what inter-individual differences in vWM capacity actually account for vWM demands related to the task or vWM demands related to language-specific processes. In order to dissociate task-related from language-specific contributions to the difficulties in sentence processing in old age, future research may compare the results from offline task designs to those of task designs that tap into real-time processing. That is because age differences in sentence processing also vanish from time to time when tasks tap into real-time, online processing, which minimizes task-related processing demands (e.g., Waters & Caplan, 2001).

Above and beyond inter-individual differences in task-related cognitive functions, tasks may also constrain sentence processing by shifting the focus towards one specific linguistic process. For instance, the task may direct the focus to syntactic or semantic information. As mentioned before, semantic processing has been suggested to yield highly memorable, deeply encoded memory traces, while syntactic processing has been suggested to lead to less memorable, shallow encoded memory traces (e.g., Bobrow & Bower, 1969; Craik & Lockhart, 1972; Craik & Tulving, 1975; Jacoby et al., 1979; Kamp & Zimmer, 2015; Rosenberg & Schiller, 1971; Schulman, 1971; Treisman & Tuxworth, 1974). Tasks that emphasize semantic processing have been suggested to enhance older adults' performance (e.g., Stine-Morrow, Noh, & Shake, 2010), while tasks that deemphasize semantic processing have been shown to yield greater error rates in older than younger adults (e.g., Tun et al., 1998). Hence, as in all three studies of this thesis, tasks that deemphasize semantic processing and instead shift the focus to syntactic processing may compromise sentence processing in old age. However, emphasizing syntactic information could also deepen syntactic memory traces (e.g., Gao, Levinthal, & Stine-Morrow, 2012; Stine-Morrow et al., 2010). It remains an open question whether older adults may be disadvantaged when tasks focus on the processing of syntactic information. Overall, for a better understanding of age differences in sentence processing, future studies should use tasks that tax task-related cognitive functions minimally without emphasizing any specific language process.

5.7 Future Directions

On the basis of the findings of this thesis new questions arise within the current debate on the effects of healthy aging on sentence processing. First, the finding that older adults' sentence comprehension difficulties can already be predicted by alterations of the electrophysiological network at rest (Beese et al., 2017) raises the relevance of resting-state networks for task-related networks. Second, functional brain aging, as reflected by age differences in the electrophysiological networks dynamics at rest (Beese et al., 2017) and task (Beese et al., submitted), may be considered as a response to structural brain aging. Third, as functional brain aging continues throughout life, future studies may benefit from cross-sectional study designs that include more than two age groups and instead assess individuals from each decade of life. Discussions about these three points will illustrate the multifaceted nature of age-related language preservation and decline.

First, future studies may examine the relevance of altered resting-state networks for task-related networks. That is because age differences were found in the resting-state EEG signal (Beese et al., 2017) and the task-related EEG signal (Beese et al., submitted). Resting-state EEG has a very high test-retest reliability and hence stability (e.g., Näpflin, Wildi, & Sarnthein, 2007). As an individual's spectral fingerprint, it may serve as an index of biologically-based, stable inter-individual differences within and across different ages (e.g., Ma et al., 2015; Nunez, 1981; Shah et al., 2017). In this thesis, the resting-state EEG signal was used to extract the individual alpha peak frequency as an index of inter-individual differences at rest to adjust frequency band ranges (Beese et al., 2017; Beese et al., submitted) that have been related to various cognitive functions (Chapter 1.4.1; e.g., Heister et al., 2013; Reichert et al., 2016; Roca-Stappung et al., 2012). Otherwise, for the purposes of this thesis, the resting-state and task-related EEG data were separately analyzed by different means (for further information on the data preprocessing, see the Methods section both in Chapter 2 and 3). However, it was recently shown that age-related sentence comprehension difficulties may be further explained by some shared variance of resting-state and task-related EEG networks subserving sentence processing (e.g., Cole, Bassett, Power, Braver, & Petersen, 2014; Geerligs, Rubinov, Cam, & Henson, 2015). This variance may differ between younger and older adults as older adults have been shown to have greater difficulties to deactivate the resting-state network during task performance (e.g., Grady, Springer, Hongwanishkul, McIntosh, & Winocur, 2006; Lustig et al., 2003; Persson, Lustig, Nelson, & Reuter-Lorenz, 2007). In other words, brain networks in older adults are not easily forced out of their resting state compared to younger adults (e.g., Garrett, Kovacevic, McIntosh, & Grady, 2013). This suggests less engagement of task-specific networks in older than younger adults (e.g., Geerligs, Saliasi, Maurits, & Lorist, 2012; Grady, 2012; Grady et al., 2010; Petti et al., 2016) and may potentially imply a larger overlap between resting-state and task-related networks in older than younger adults. Therefore, the observed age-related sentence comprehension difficulties in Beese et al. (2017) and Beese et al. (submitted) may also be associated with greater difficulties to deactivate the resting state in old age (e.g., Geerligs et al., 2015). For instance, in Beese et al. (submitted), older adults' encoding success was predicted by an upregulation of alpha power. While it may be hypothesized that such an upregulation may force older adults out of the resting state, this is purely speculative and requires further research that compares resting-state and task-related EEG signals more directly to evaluate the role of resting-state networks for task-related networks during language processing.

Second, future research on functional brain aging should take inter-individual differences in structural brain aging into account. That is because inter-individual differences in structural brain aging may constrain the mechanism of functional brain aging at work (e.g., Barulli & Stern, 2013; Cabeza et al., 2018). For instance, Tyler et al. (2010) found that older adults' gray matter atrophy in the left-hemispheric fronto-temporal language network (i.e., structural brain aging) was compensated for by increased neural activity in its right-hemisphere homologue (i.e., functional brain aging). This pattern yielded preserved sentence processing in older adults and hence supports the mechanism of compensation. However, this mechanism of functional brain aging crucially differs depending of the circumstances of structural degradation (such as gray matter atrophy) or structural preservation (i.e., brain reserve; Stern, 2006). Both have been shown to yield different functional manifestations with either preserved (i.e., cognitive reserve) or detrimental cognitive performance (for a review, see Anthony & Lin, 2018). Therefore, mechanisms of functional brain aging may be best examined at different stages of structural brain aging. That is, future research should take inter-individual differences in structural brain aging into account while matching older and younger adults' behavioral performance. However, it may be difficult to find healthy younger adults with poor performance. Therefore, alternatively, instead of matching younger and older adults by their task performance, future research may aim for equivalent performance by adapting the task demands for each age group. This assures that the cognitive process of interest is assessed rather than increased task demands. This may give some indication of which functional brain mechanisms (e.g., compensation or dedifferentiation) underlies the effects of healthy aging on sentence processing.

Third, as inter-individual differences in functional and structural brain aging persist throughout life, cross-sectional studies can often not capture individual developmental changes. While the inclusion of younger and older adults in cross-sectional designs may already give first indications on age differences, such two-group designs assume a linear change across the lifespan, possibly overlooking non-linear changes. In contrast, longitudinal studies can reveal linear as well as non-linear effects of age within and across age groups. However, longitudinal studies over several decades from young to old age are obviously an exception. Therefore, if resources allow for it, it would be a good compromise for future studies to include a good number (e.g., ~ 30) of individuals per decade into a cross-sectional study design. This allows for a consideration of linear and non-linear age effects (for a good example, see Bender & Raz, 2015; Bender et al., 2016).

5.8 Conclusion

Across the lifespan, successful language comprehension is crucial for continued participation in everyday life. However, despite older adults' life-long experience with language, healthy aging affects language comprehension in a combination of language preservation and decline. To date, our understanding of these two complementary facets is incomplete and unclear. Aiming for a better understanding, this thesis examined the effects of healthy aging on sentence comprehension. As to that, sentence comprehension was related to alterations of the language-specific and domain-general electrophysiological network dynamics at rest (see Chapter 2, Beese et al., 2017), to alterations of the electrophysiological correlates of sentence encoding (see Chapter 3, Beese et al., 2019), and the benefit of semantic and syntactic constraints to counteract older adults' vWM limitations (see Chapter 4, Beese et al., 2019). The results revealed that age-related difficulties in sentence comprehension were predicted by alterations of resting-state networks relevant for vWM, while the functional integrity of the core sentence-processing network remained preserved across the lifespan. Therefore, the prerequisite for sentence processing already changes at rest. In a similar vein, older adults' sentence comprehension difficulties were also associated with alterations of the electrophysiological network underlying the encoding of sentences into vWM. However, general vWM limitations did not further compromise the effects of healthy aging on syntactic and semantic processing. Instead, healthy aging affected syntactic but not semantic processing regardless of older adults' limited vWM capacity. In sum, the findings of this thesis revealed a combination of age-related preservation and decline: while semantic processing remains preserved, syntactic processing declines and the overall decline in sentence processing is further associated with limitations in domain-general cognitive functions that typically support language processing. This suggests an increase of the relative importance of both semantic processing and domain-general cognitive functions for successful language comprehension in healthy aging. Thereby, this thesis deepens and extends our understanding of the effects of both language-specific and domain-general neurocognitive aging on sentence processing. On the basis of these findings, future studies are encouraged to dissociate distinct language-specific processes from one another and from task-related cognitive processes. This will help to isolate the language-specific process of interest and will minimize confounding contributions from domain-general cognitive processing efforts.

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Appendix A

Supplements: Details on Methods

This chapter will first describe the neuropsychological test battery used in the here presented thesis. After both strength and limitations of the methodological approaches will be highlighted.

A.1 Neuropsychological Test Battery

Throughout the three studies of the here presented thesis, a large battery of neuropsychological tests was administered to detect general cognitive impairment as well as more specific domain-general cognitive abilities that crucially support sentence processing but are known to decline with advancing adult age. The neuropsychological testing took ∼3 hours.

A.1.1 General Cognitive Functioning

The Mini Mental State Examination 2 (MMSE-2 Folstein, Folstein, White, & Messer, 2010) consists of 30 questions assessing short-term and long-term memory, temporal and spatial orientation, arithmetic, naming, comprehension, reading, writing and drawing. Participants scoring below 27 were excluded as such scores indicate some cognitive impairment (such as dementia). The total test took about 15 minutes.

A.1.2 Memory

Sentence processing is crucially supported by memory processes (see Chapter 1.2.2). For instance, as sentences unfold, more and more language-specific information (i.e., semantic, syntactic and phonological information) have to be encoded and retained until the sentence has been processed in full. Hence, sufficient memory capacity is important to for successful sentence comprehension (e.g., Just & Carpenter, 1992). For this reason, short-term memory capacity of both meaningful (Digit Span Forward Task) and meaningless items (Non-Word

Repetition Span Task) was assessed to quantify the ability to retain phonological information with or without the influence of semantics (i.e., meaningfulness), respectively. Moreover, the retention of language-specific information may be interfered by the simultaneous encoding of new information which increases the executive demands (e.g., Lewis et al., 2006). Therefore, vWM was assessed under lower executive demands (Digit Span Backward Task) and higher executive demands (Counting Span Task).

Digit Span Forward and Backward

The Digit Span Forward and Backward Task (Aster, Neubauer, & Horn, 2006) measure the repetition of sequences of digits. Thereby, the Digit Span Forward reflects phonological storage capacity, whereas the Digit Span Backward additionally associates with higher central executive demands. Both tasks required participants to memorize and repeat out loud auditorily presented sequences of digits. Starting from two digits, the number of digits increases by one to maximally nine digits, until participants repeat two consecutive sequences of the same length incorrectly. Testing first the Digit Span Forward, then Backward took about 10 minutes.

Non-word Repetition Span

The Non-Word Repetition Span Task (i.e., Mottier Welte, 1981) measures the phonological retention of non-words, that is meaningless but phonological correct words. In comparison to the Digit Span Forward Task, the Non-Word Span Task measures the phonological storage capacity in isolation of semantic confounds. Participants were required to memorize and repeat out loud the auditorily presented non-words. Starting from a non-word length of two syllables (e.g., *rela*), the syllable length is increased by one after every sixth non-word. When the last two non-words of one length and the first two non-words of the following increased length were repeated incorrectly, the test was terminated. The number of total words accounts as the raw score. The Non-Word Repetition Span Task took about 10 minutes.

Counting Span Task

The Counting Span Task (Case, Kurland, & Goldberg, 1982) measures vWM capacity under an increasing degree of executive demands. Participants were asked to count out loud green target circles while inhibiting yellow distractor circles as they observed pictures with both green and yellow circles on a screen. Counting out loud prevented participants to subvocally rehearse the total counts. Participants needed to retain the total count of green circles in order to recall them after all pictures of each trial were presented. For instance, if two pictures showed four and six green circles, respectively, participants needed to recall first four, then six. Starting from one picture, the set size increased by one after each set size was repeated three times (e.g., three times two pictures). Participants needed to correctly recall the sequence at least one of three times otherwise the test was terminated. The maximum set size was five. An individual's span size was determined by the highest set size for which participants remembered at least two out of three trials correctly. An additional 0.3 points was added per trial of a set size for which participants did not remember at least two trials correctly. The Counting Span Task took about 15 minutes.

A.1.3 Attention

Selective attention plays a crucial role for sentence processing (e.g., Fedorenko, 2014). Specifically, the ability to inhibit irrelevant information while focusing on the relevant information is a crucial determinant for successful sentence comprehension (e.g., Lewis et al., 2006).

Auditory Flanker Task

The Auditory Flankers Task (e.g., Chan, Merrifield, & Spence, 2005; Huang, Rossi, Hamalainen, & Ahveninen, 2014) assesses selective attention. Participants have to allocate their attention to task-relevant target information while inhibiting task-irrelevant information (i.e., the auditory flankers). Reaction times to the target are then measured and compared for conditions of same and different target-and-flanker combinations.

The design and procedure used in Beese et al. (2017) and Beese et al. (submitted) resembles that reported by Huang et al. (2014). In brief, participants were seated in front of three loudspeakers: one to the left (45°), one to the right (45°) and one straight ahead, all in 40 cm distance. Participants were asked to respond to the target sound from the speaker straight ahead of them, via a button box with designated "*A*" and "*O*" buttons (for half the participants "*A*-*O*", for the other half "*O*-*A*"; counterbalanced across gender and age group). The target sounds were half of the times "*A*"s, otherwise "*O*"s. The flankers were either both "*A*"s or both "*O*"s, one flanker 3.1 semitones higher, the other 3.1 semitones lower than the target sound, counterbalanced in position. Flankers and targets were half of the trials congruent ("*Ahigh – A – Alow*" or "*Ohigh – O – Olow*"), half incongruent ("*Alow – O – Ahigh*" or "*Olow – A – Ohigh*"). No three consecutive trials had the same target, semitone position or condition of congruency. All sounds lasted for 400 ms but the target was presented 300 ms post-flankers onset in order to increase sound discrimination (for more details, see Huang et al., 2014). The inter-trial interval was 500-1000 ms. During and between trials a fixation cross was presented. The task consisted of 200 trials and took about 20 minutes.

A.1.4 Intelligence

Both verbal intelligence (Vocabulary Task, Similarities Task) and non-verbal intelligence (Matrices Task, Block Task) were assessed using subtests of the Wechsler Adults Intelligence Scale(WAIS; Aster et al., 2006). Together, the four tests took about 90 minutes.

Vocabulary Task

The Vocabulary Task assesses semantic knowledge. Participants were asked to define a maximum of 33 words, explaining their meaning. The test was terminated when six consecutive words were incorrectly defined. This test lasted about 40 minutes.

Similarities Task

The Similarities Task also assesses semantic knowledge, specifically the ability of semantic abstraction. Participants were asked to find the semantic similarity between each of the 19 word pairs, such as “piano” and “drums”. The test was terminated if participants could not find the similarity in four consecutive pairs. This test took about 10 minutes.

Matrices Task

The Matrices Task assesses abstract reasoning and the recognition of analogies. Participants were presented with matrices that were each missing one piece. To correctly complete a matrix, participants had to identify the only correct solution out of five options. The test consists of 26 matrices but was terminated when participants did not identify the solution or selected an incorrect option in four consecutive matrices or four out of five matrices. This test took about 30 minutes.

Block Task

The Block Task assesses spatial awareness. Participants were asked to replicate a pattern out of dice. The complexity of those patterns increased with the number of dice (first four, then nine). In total 14 patters had to be replicated. However, the test was terminated when participants incorrectly replicated three consecutive patterns. This test took about 10 minutes.

A.1.5 Audiometry

On top of the neuropsychological test battery, hearing abilities were assessed for all participants who took part in the studies of Beese et al. (2017) and Beese et al. (submitted). This is because any degree of hearing loss could reduce the cognitive resources available for auditory language processing (e.g., Wingfield, Tun, & McCoy, 2005). Therefore, a pure tone audiometry was administered to assure that older adults were not disadvantaged by any age-related hearing loss during the auditory sentence comprehension task.

First, participants were seated and asked to wear sound-proof headphones. Participants responded to any sound that were truly perceived. Sounds started from 1000 Hz with a volume of 40 dB, going down in steps of 10 dB, until participants could not perceive the sound anymore. Then the volume was increased in steps of 5 dB, playing each sound for three times, until participants could hear the sound again. This procedure was then repeated for frequencies of 2000 Hz, 3000 Hz, 4000 Hz, 6000 Hz, 8000 Hz, 500 Hz, and 250 Hz, in this particular order. Overall, this common procedure took about 15 minutes.

A.2 Data Analyis

This section will highlight some of the strengths and limitations of the data analyses used in Beese et al. (2017) and Beese et al. (submitted).

A.2.1 Optimized Data Cleaning Using Independent Component Analysis

A number of different artifacts were removed during data cleaning (Beese et al., 2017; Beese et al., submitted): slow voltage drifts, vertical and horizontal eye movements, heartbeats, and muscle contractions. Slow voltage drifts can be removed using an adequate high-pass filter. Eye movements and heartbeats can be detected with an independent component analysis (ICA) and eliminated by removing the corresponding independent components (IC). This leaves only muscle artifacts, for the removal of which whole segments need to be removed from the data. Using this combination of procedures reduces the amount of data loss during data cleaning.

The ICA is a blind source-separation algorithm that decomposes the EEG time series into a set of independent components that correspond to independent sources of the data (Makeig, Bell, Jung, & Sejnowski, 1996). Thereby, mutual information between these component is minimized. The signal can be maximally decomposed into as many sources as there are channels. However, the signal from each channel does typically not correspond to only one source which does create some degree of shared variance and hence interdependence between channel pairs. Therefore, the signal may be decomposed into fewer independent components (IC) to remove this redundancy. This also speeds up the ICA analysis. In order to decompose the channels into fewer ICs, a dimension reduction of the signal is required, for instance, via a principle component analysis (PCA). The PCA would remove any redundancy by transforming the data into an equal number of linearly-uncorrelated samples.

ICs corresponding to artifacts can be detected based on the components' waveform morphology, power spectrum, and scalp topography (see Figure A.1). For instance, the ICs corresponding to eye movement typically peak at 1 Hz at anterior sites. However, the IC corresponding to vertical eye movement has a central anterior distribution while that corresponding to horizontal eye movement is distributed to the left and right anterior sites. In addition, the waveform morphology of the IC corresponding to vertical eye movement resembles high amplitude deflections while that corresponding to horizontal eye movements resembles rectangular-like shapes. Another example is the IC that corresponds to heartbeats: it is distributed at two opposite sides of the outer rim of the scalp and has regular amplitude deflection in the waveform morphology. Moreover, electrode noise can also be detected with the help of ICA. An IC reflecting electrode noise is distributed around one single electrode, without creating a dipole. Its waveform has pointy and sharp deflections. Its frequency spectrum has no clear peak and larger amplitudes at higher frequencies.

The performance of an ICA can be optimize by means of prior high-pass filtering (Winkler, Debener, Muller, & Tangermann, 2015). That is, compared to a 0.5 Hz high-pass filter, a 1 Hz and 2 Hz high-pass filter increase the SNR, the classification accuracy, and also the ICA decomposition. However a 0.5 Hz high-pass filtered data provides more information for subsequent statically analysis. Therefore, in Beese et al. (2017) and Beese et al. (submitted), the raw data were filtered at 0.5 Hz and separately at 1 Hz, creating two high-pass filtered data sets, to optimize data cleaning. The ICA was trained on the 1 Hz filtered data, while the weights were applied to the 0.5 Hz filtered data from which also the artifactual ICs were removed. While this worked well for most data sets, I found that in some data sets few drifts remained in the 0.5 Hz high-pass filtered data that were removed in the 1

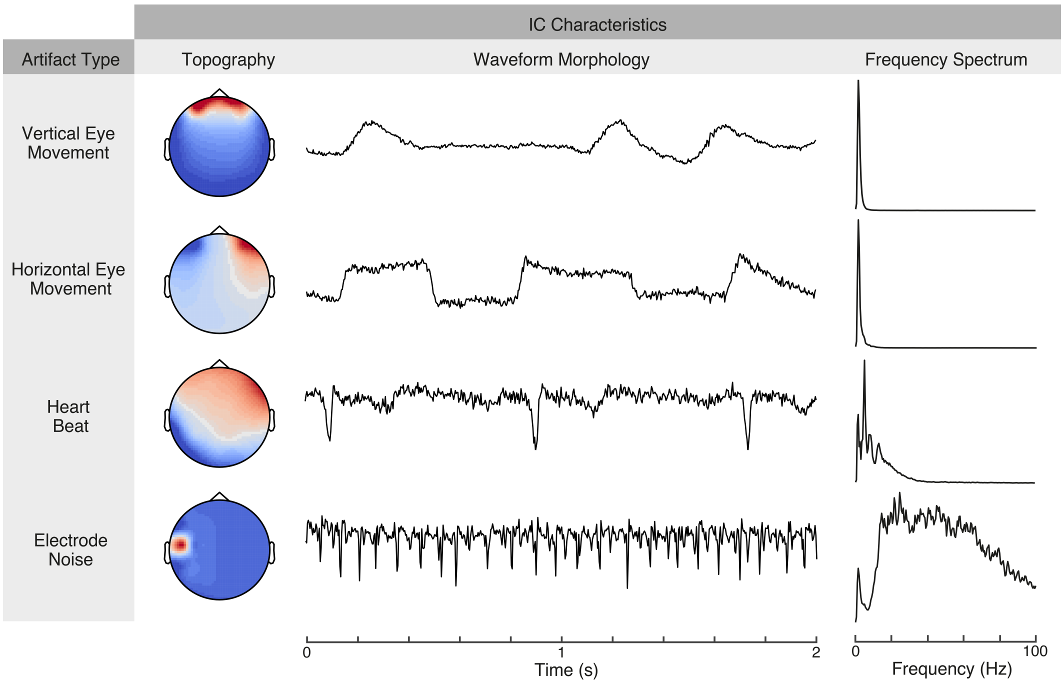

Figure A.1: Overview of the topographic, waveform and frequency characteristics of independent components reflecting typical EEG artifacts.

Hz high-pass filtered data. Therefore, in some cases, the data cleaning had to be redone, removing such drift from the beginning.

A.2.2 The Importance of Data Normalization

Baseline correction is a standard procedure to normalize the signal (Luck 2005). There are at least five reasons why the signal should be baseline-corrected (Cohen, 2014): 1) there is inter-individual variance in absolute power values, 2) absolute power has a 1/f distribution and is hence not normally distributed, 3) the event-related signal needs to be dissociated from background noise, 4) absolute power cannot be compared across frequencies, and 5) the visualization of absolute power values across different frequency bands would be difficult. In other words, baseline correction enables the comparison of data across conditions, electrodes, frequencies, and participants. In an event-related design, most commonly baseline activity from an interval pre-stimulus onset is selected to normalize the post-stimulus activity. Therefore task-related activity must be interpreted relative to the background activity. As both signal and baseline interval are equally affected by the 1/f scaling, a baseline correction of the signal would remove this constancy. In a resting-state design, there is no obvious baseline interval that the signal can be compared to. Often the data is log– or z-transformed and/or divided by the total power (log data = log(raw data / mean data), creating normalized absolute or relative power values, respectively. In line with this procedure, in Beese et al. (2017), I have opted for a log-transformation of the absolute resting-state EEG power values (e.g., Maltez, Hyllienmark, Nikulin, & Brismar, 2004; Näpflin et al., 2007; Prichep et al., 2006). Therefore, I have only normalized, but not baseline-corrected the signal. A baseline correction was not necessary as my interest lay in the theta band only and the 1/f scaling would only induce large power differences between different frequencies in wide frequency bands (e.g., gamma 30–80 Hz) or across several frequency bands (e.g., theta to beta: 4–30 Hz).

In contrast, in event-related designs, EEG power is often normalized via a baseline correction. In Beese et al. (submitted), the event-related EEG power was normalized by considering the relative change from condition-specific pre-stimulus baseline activity to condition-specific post-stimulus event-related activity (baseline corrected data = (raw data - baseline) / baseline) in order to be able to compare the results to our previously published results of the younger adults (Vassileiou, Meyer, Beese, & Friederici, 2018).

As I have found age effects in two differently normalized data sets (absolute resting-state power versus relative event-related power), it is not possible to compare the two effects without adapting the normalization of one data set to the other. As this likely affects the results and as this was not the interest of my work, I refrained from the conjunction. However, future studies including both resting-state and event-related data may chose an identical normalization procedure for both data sets in order to allow for combined analysis. Despite all advantages, normalization through baseline correction comes with two problems: 1) the arbitrariness of baseline interval chosen (e.g., Alday, 2019) and 2) the á priori assumption that there are no systematic differences in the baseline interval between conditions (e.g., Urbach & Kutas, 2002, 2006). With respect to 2) if there were systematic differences, a baseline correction would induce baseline activity into the task-related activity. This would possibly introduce non-existing condition differences. Therefore, future studies may consider including baseline activity into the statistical analysis as was recently suggested by Alday (2019).

A.2.3 The Importance of Alpha Peak Adjustment

Oscillatory activity within specific frequency bands have been shown to bear functional relevance for a variety of cognitive abilities (such as memory or language: Klimesch, 1999; Meyer, 2017, respectively). As the electrophysiological signal slows does with increasing age, the frequency range that bear functional relevance for cognitive abilities may need to be adjusted. At best the signal's frequency spectrum is adjusted with respect to the individual alpha peak (IAF) because of its intra-individual stability (Dustman et al., 1999; Grandy et al., 2013; Klimesch, 1999; Scally et al., 2018). However, across the lifespan, the IAF decreases from approximately 10–10.5 Hz in younger adults to 9–9.5 Hz in older adults (∼70years of age; see Chapter 1.4), yielding a possible downward shift in functional frequency bands. As for the procedure, the typical alpha band range between 8–12 Hz is extended to 7–14 Hz in order to cover the individual differences across age groups. The power within these frequencies is extracted from posterior and occipital electrodes: Pz, P3, P4, P5, P6, P7, P8, P9, P10, POz, PO3, PO4, PO7, PO8, O1, O2, and Oz, which relate to wakefulness at a state of relaxation and rest (e.g., Klimesch, 1999; Niedermeyer, 1993). It was argued that the "real" alpha peak can be determined by the alpha peak attenuation when opening the eyes (EO) after a resting state with eyes closed (EC Klimesch, 1999; Posthuma, Neale, Boomsma, & De Geus, 2001). Therefore, EO power should be subtracted from EC power. The maximum peak within the EC–EO difference spectrum constitutes the IAF. The IAF is then used as anchor point to constrain the frequency band of interest into a range from (IAF – 6 Hz) to (IAF – 2 Hz), shifting each individual's power spectrum. Then the oscillatory power is averaged across individual frequencies within each functional frequency bands.

A.2.4 Source Reconstruction and its Pitfalls

Even though the EEG does not offer high spatial resolution, underlying sources can be reconstructed. That is, the signal at scalp level can be attributed to distinct sources by means of spatial filtering. Scalp-level EEG signals can be localized with high spatial specificity using beamforming approaches. Beamforming is a spatial filtering method that assumes that the time courses of different sources are uncorrelated. That is, the beamformer linearly combines the spatially sampled time courses from each channel. In this approach, the brain is divided into 3D grid points at which source activity is estimated from the covariance of data. In the frequency domain, the beamformer method of choice in Beese et al. (2017) is the Dynamical Imaging of Coherent Sources (DICS Gross et al., 2001). This method estimates source activity from the covariance matrix of the data constituted by the cross-spectral densities (CSD) of all sensor combinations, a byproduct of the Fast Fourier Transform.

For this approach, at first, a forward model has to be constructed for each participant. However, without information on electrode positions, template head models have to be computed, including the segmentation of the head into scalp, skull, and brain. When the individual structural brain image is unavailable, a structural brain template can be used as in Beese et al. (2017). In this case, a head model is best constructed using the boundary element model (BEM) which assumes homogeneous volume conductivity. Afterwards, the head space is divided into 3D grid points. Based on the head model, a spatial filter is constructed from the CSD at each grid point for a specific frequency or average of frequencies in a specific band. Thereby it is important to correct for the central head bias (i.e., strongest noise projection towards the center of the head). When all data stem from a single condition, the signal (as in resting-state EEG Beese et al., 2017) needs to be normalized with an estimate of the spatially inhomogeneous noise. That is, the estimated power at each source is normalized by the estimated power at each source (corrected source activity = source activity / noise). Now the estimated source activity at each grid point can be superimposed onto a structural brain template.

While the beamformer method localizes distinct sources of the signal, it does not provide information on their interdependence. Post-hoc, the interdependence, or functional coupling, of the time courses of the spatially distinct sources can be tested using a source-level coherence analysis (as described in Beese et al., 2017). Source-level coherence is a measure of functional coupling between EEG sources. Coherence refers to the linear correlation in the time-frequency domain between pairs sources (e.g., Bowyer, 2016; French & Beaumont, 1984). However, coherence between sources decays with increasing inter-source distance due the contribution of neighboring sources to the same signal (i.e., a problem arising due to volume conduction). Therefore, the results may be confounded by an underestimation of inter-network and an overestimation of intra-network coherence. Therefore, a post-hoc source separation analysis using ICA can be conducted to examine the temporal independence of spatially distinct sources (as described in Beese et al., 2017).

List of Abbreviations

BA	Brodmann Area
BEM	Boundary Element Model
CRUNCH	Compensation-Related Utilization of Neural Circuits Hypothesis
CSD	Cross-Spectral Densitiy
DICS	Dynamical Imaging of Coherent Sources
EC	Eyes Closed
EEG	electroencephalogram
ELAN	Early Left Anterior Negativity
EO	Eyes Open
EOG	Electrooculogram
ERP	Event-Related Potential
FDR	False Discovery Rate
FFT	Fast Fourier Transform
FMT	Frontal Midline Theta
IAF	Individual Alpha Peak
IC	Independent Component
ICA	Independent Component Analysis
IFG	Inferior Frontal Gyrus
IPL	Inferior Parietal Lobule
ITG	Inferior Temporal Gyrus

ITS	Inferior Temporal Sulcus
LAN	Left Anterior Negativity
LNR	Later Not Remembered
LR	Later Remembered
MMSE-2	Mini Mental State Examination 2
MTG	Middle Temporal Gyrus
NP	Noun Phrase
PASA	Posterior-to-Anterior Shift in Aging
PCA	Principle Component Analysis
PFC	Prefrontal Cortex
PM	Premotor Cortex
RS	resting state
SME	Subsequent Memory Effect
STG	Superior Temporal Gyrus
STS	Superior Temporal Sulcus
vWM	verbal working memory

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Summary

Across the lifespan, successful language comprehension is crucial for continued participation in everyday life. Language comprehension encompasses both language-specific processes (e.g., semantic and syntactic processes) and domain-general cognitive processes (e.g., verbal working memory, vWM) that support language comprehension (e.g., Campbell & Tyler, 2018; Fedorenko, 2014; Wingfield & Grossman, 2006). While language experience increases with age, in principle, most domain-general cognitive functions decline in healthy aging. This may explain why previous studies revealed diverging effects of healthy aging on language comprehension: the preservation and the decline of language comprehension on both the cognitive and the neural level (Burke & Shafto, 2008; Diaz et al., 2016; Peelle, 2019; Shafto & Tyler, 2014; Wingfield & Grossman, 2006). To date, our understanding of the effects of healthy aging on language comprehension remains incomplete and unclear.

Sentence comprehension has been found to remain preserved in healthy aging when sentences are simple and short (e.g., Gilchrist et al., 2008; Wingfield et al., 1985). In contrast, sentence comprehension has been shown to decline in healthy aging when sentence processing becomes vWM-demanding (e.g., Feier & Gerstman, 1980). Therefore, vWM plays a key role in sentence comprehension. It is presumed that sentence comprehension relies on the successful encoding of sentences into vWM. However, as vWM resources decline with advancing age (e.g., Bopp & Verhaeghen, 2005), vWM resources may become insufficient in old age to successfully encode sentences into vWM (e.g., Friedman & Johnson Jr., 2014). However, it remained an open question whether older adults' sentence comprehension difficulties may be related to deficient sentence encoding. Such difficulties may be attenuated when language-specific information is exploited to reduce the vWM load. That is, semantic and syntactic information can be used to group single words to word groups which reduces the vWM load. It also remained an open question whether older adults differ in the extent to which they use language-specific information to cope with their vWM limitations.

The overarching goal of the here presented thesis was to contribute to the understanding of the effects of both language-specific and domain-general neurocognitive aging on language

comprehension using the electroencephalogram (EEG). In contribution to this aim, three major research questions were addressed:

(1) Do the prerequisites for sentence comprehension change across the lifespan as electrophysiological networks in the brain at rest change with age?

(2) Do alterations of the electrophysiological correlates of sentence encoding compromise sentence comprehension in healthy aging?

(3) Are semantic and syntactic information differentially used by older and younger adults to reduce the vWM load?

Answers to these questions will be given by the here presented work and will contribute to a better understanding of the diverging nature of language preservation and decline in healthy aging.

In the first study, the effects of healthy aging on the electrophysiological basis of sentence processing in the brain at rest were investigated (Beese et al., 2017). It was hypothesized that sentence comprehension difficulties may emerge in older adults if the functional integrity of the language-specific and/or the domain-general electrophysiological network at rest becomes compromised. That is, in other words, if the resting-state networks change across the lifespan, the prerequisites for sentence comprehension may also change with age. Previous studies proposed that quasi-rhythmic oscillatory activity in the theta frequency band (4–8 Hz) bears functional relevance for both language-specific processes and domain-general cognitive abilities, specifically vWM, in the presence of a task (for review, see Meyer, 2017). However, to date, there is a critical gap in our understanding of the functional relevance of resting-state theta oscillations for language comprehension, how the underlying resting-state theta networks change across the lifespan and how such changes may affect language comprehension in healthy aging. To fill this gap, in Beese et al. (2017), resting-state theta power was related to sentence comprehension across the lifespan. To this end, first the EEG was recorded at rest, then both language-specific and domain-general cognitive abilities were assessed from younger, middle-aged and older adults (25, 43, 65 years). The results showed that resting-state theta power within the left dorso-frontal language network predicts sentence comprehension independently of age. In contrast, older adults' sentence comprehension difficulties were found to be associated with a decline in resting-state theta power within an electrophysiological network relevant for vWM that supports sentence comprehension. Hence, two distinct resting-state theta networks support sentence comprehension across the age trajectory, but only the network related to vWM yields older adults' sentence comprehension difficulties. This suggests that when the prerequisites for sentence comprehension change with age at rest, sentence comprehension difficulties may emerge.

In the second study, this key role of vWM for sentence comprehension in healthy aging was further examined (Beese et al., submitted). This study was motivated by the common presumption that accurate sentence comprehension relies on the successful encoding of sentences into vWM. Comprehension difficulties may specifically arise when the vWM capacity to encode sentences into vWM declines in healthy aging. To this end, the EEG was recorded while younger, middle-aged and older adults (24, 43, 65 years) listened to long sentences that they needed to encode and remember for a subsequent auditory sentence comprehension task. The accuracy of the given response served as an index for the encoding success. The difference in oscillatory power between correctly and incorrectly encoded sentences yielded subsequent memory effects (SME) which were compared across age groups. Age differences were found in the SME within the lower alpha frequency band (8–10 Hz). Specifically, encoding success was characterized by an alpha power decrease in younger adult; that is, alpha power was smaller when sentences were correctly encoded than when sentences were incorrectly encoded. In contrast, encoding success was characterized by an alpha power increase in older adults; that is, alpha power was larger when sentences were correctly encoded than when sentences were incorrectly encoded. As oscillatory activity within the alpha band has frequently been linked to inhibition, it seems likely that the encoding success in linked to inhibition, too. Specifically, increased alpha power in older adults may indicate that older adults inhibit the encoding of detailed information that would otherwise overload their limited vWM capacity. As older adults may inhibit the encoding of detailed information, fewer details would be extracted while older adults could still focus on the gist of sentences. These results substantiate the relative importance of domain-general neurocognitive aging for sentence comprehension in healthy aging.

In the third study, it was examined whether these detrimental effects of domain-general neurocognitive aging on sentence comprehension could be attenuated through the use of language-specific information (Beese et al., 2019). That is, specifically semantic and syntactic information can be used to establish relations between words which reduces the vWM load from single word information to information about word groups. For instance, on the basis of syntactic information, the article “the” and the noun “boat” can be conjoined into the enriched syntactic representation of a noun phrase, “the boat”. In a similar manner, on the basis of semantic constraints, the representations of the adjective “blue” and the noun "boat" can be conjoined into an enriched semantic representation of a boat that is blue, "blue boat". An inefficient use of semantic and/or syntactic constraints may be related to older adults' difficulties in sentence comprehension. Hence, this third study addressed the open question whether younger and older adults differ in the extent to which they exploit semantic and syntactic information to reduce the vWM load. To this end, younger and older adults (26 and 65 years, respectively) read sentences (with syntactic constraints) or lists (without syntactic constraints) that were comprised of either real words (with semantic constraints) or pseudowords (without semantic constraints). Semantic and syntactic relations between words were emphasized by a subsequent serial order task whereby participants had to match the serial order of two words with their previous occurence. Two experiments were conducted to vary the potential benefit of language-specific constraints to reduce vWM demands. As to that, vWM demands were varied: the sequence length was increased from eight (pseudo-) words in Experiment 1 to eleven (pseudo-) words in Experiment 2. The results indicated that when vWM demands are higher, older adults do not benefit from the use of syntactic constraints as much as younger adults, while the benefit of using semantic constraints was comparable across age groups. Possibly, older adults extract less detailed syntactic information in light of their limited vWM capacity and instead focus on the gist of sentences. That is, older adult's preserved use of semantic constraints may suggest that older adults focus more on what is said (i.e., the semantic information) than how it is said (i.e., the syntactic information). This may indicate that older adults shift their focus from syntactic to semantic information to accomplish successful sentence comprehension.

Altogether the results of the here presented thesis showed that language comprehension is affected by language-specific and domain-general neurocognitive aging. In particular, the results showed that sentence comprehension difficulties emerge in older adults as the functional integrity of the electrophysiological network relevant for vWM becomes compromised either at rest or during sentence processing. Specifically, the encoding of sentences into vWM played a key role for successful language comprehension. Here, it was found that older adults accomplish successful sentence comprehension by inhibiting the encoding of detailed information, probably to avoid an overload of their limited vWM capacity. Such overload could arise if information that is just being encoded interferes with the already encoded information as this would increase the processing costs (e.g., Lewis et al., 2006). Such encoding interference has been shown to play a crucial role for sentence comprehension (e.g., Gordon et al., 2002; Lewis & Vasishth, 2005; Lewis et al., 2006). However, the ability to inhibit interference was found to be compromised in old age. Therefore, older adults may have

difficulties to inhibit the encoding of detailed information even if it yielded greater sentence comprehension success. Regardless, older adults typically still get the gist of sentences (e.g., Reder et al., 1986; Tun et al., 1998). This possibly relates to the finding that older adults do not benefit from detailed syntactic information while the benefit from semantic information is comparable across the lifespan. If older adults inhibited the encoding of detailed syntactic information, it would be more challenging to establish syntactic relations between words and group single words to word groups. This would in turn increase the processing costs in older adults. Hence, aiming for a good level of sentence comprehension, older adults may focus on what has been said (i.e., the semantic information) rather than how it was said (i.e., the syntactic information). Altogether, the overall findings converge on the detrimental effects of declining domain-general cognitive functions on sentence processing while diverging on the domain-specific cognitive functions into the preservation of the use of semantic information and the decline in the use of syntactic information. This illustrates that older adults' comprehension difficulties are associated with both language-specific and domain-general neurocognitive aging. However, future research is needed to substantiate the proposed links between the encoding, the inhibition and the extraction of language-specific information.

Zusammenfassung

Das Verstehen von Sprache bleibt auch im Alter wichtig, um weiterhin aktiv am Leben teilnehmen zu können. Zum Sprachverstehen gehören sowohl sprachspezifische Verarbeitungsprozesse (z.B. semantische und syntaktische Prozesse) als auch allgemeine kognitive Prozesse, die nicht sprachspezifisch sind, aber das Sprachverstehen unterstützen (z.B. Arbeitsgedächtnlisleistungen Campbell & Tyler, 2018; Fedorenko, 2014; Wingfield & Grossman, 2006). Während mit dem Alter das sprachspezifische Wissen prinzipiell zunimmt, nimmt die Funktionalität der allgemeinen kognitiven Prozesse ab. Dieser altersbedingte Abbau allgemeiner kognitiver Prozesse könnte erklären, warum bisherige Studien zu unterschiedlichen Ergebnissen gekommen sind. Einerseits fanden bisherige Studien einen Erhalt und andererseits eine Abnahme des Sprachverstehens auf kognitiver und neuronaler Ebene im Alter (Burke & Shafto, 2008; Diaz et al., 2016; Peelle, 2019; Shafto & Tyler, 2014; Wingfield & Grossman, 2006). Bislang ist unser Verständnis der Auswirkungen des gesunden Alterns auf das Sprachverstehen jedoch unvollständig und lückenhaft.

Ältere Erwachsene haben in der Regel keine Probleme, einfache Sätze zu verstehen (z.B., Gilchrist et al., 2008; Wingfield et al., 1985). Allerdings wird das Verstehen erschwert, sobald Sätze das Arbeitsgedächtnis beanspruchen (z.B., Feier & Gerstman, 1980). Dabei nimmt man an, dass sprachliche Informationen zuerst in das Arbeitsgedächtnis enkodiert werden müssen, um am Ende Satzinhalte verstehen zu können. Da jedoch die Kapazität des Arbeitsgedächtnisses mit dem Alter sinkt (z.B., Bopp & Verhaeghen, 2005), kann es dazu kommen, dass Satzinformationen unzureichend in das Arbeitsgedächtnis enkodiert werden und dadurch das Verstehen von Sätzen erschwert wird (z.B., Friedman & Johnson Jr., 2014). Diese Schwierigkeiten können jedoch erleichtert werden, indem die Informationsmenge durch sprachspezifische Prozesse reduziert wird. Dabei können semantische und syntaktische Informationen dazu genutzt werden, einzelne Wörter zu Wortgruppen zusammenzufassen, um so die Belastung des Arbeitsgedächtnisses zu reduzieren.

Das übergeordnete Ziel der vorliegenden Arbeit war es, Auswirkungen altersbedingter Veränderungen sprachspezifischer und allgemeiner kognitiver Prozesse auf das Sprachverstehen besser zu verstehen. Dabei wurden drei Kernfragen bearbeitet:

(1) Ändern sich die Voraussetzungen für das Sprachverstehen im Alter, indem sich elektrophysiologische Netzwerke schon im Ruhezustand mit dem Alter verändern?

(2) Gibt es einen Zusammenhang zwischen Veränderungen der elektrophysiologischen Korrelate des Enkodierens von Satzinformationen und dem Sprachverstehen im Alter?

(3) Werden syntaktische und semantische Informationen im Alter unterschiedlich genutzt, um die Arbeitsgedächtnisbelastung zu reduzieren?

Die Antworten auf diese Fragen, die in der vorliegenden Arbeit gegeben werden, tragen zu einem besseren Verständnis über mögliche Faktoren des Erhalts bzw. Abbaus des Sprachverstehens im Alter bei.

In der ersten Studie wurde untersucht, ob sich Veränderungen elektrophysiologischer Netzwerke im Ruhezustand auf das Verstehen von Sätzen im Alter auswirkt (Beese et al., 2017). Die Hypothese war, dass Schwierigkeiten mit dem Satzverstehen im Alter entstehen könnten, wenn die funktionale Integrität elektrophysiologischer Netzwerke, die den sprachspezifischen und/oder allgemeinen kognitiven Prozessen zu Grunde liegen, beeinträchtigt ist. Diese Hypothese beruhte auf der Annahme, dass wenn sich bestimmte elektrophysiologische Netzwerke im Ruhezustand verändern, ändern sich auch die Grundvoraussetzungen für das Satzverstehen mit dem Alter. Bisherige Studien hatten gezeigt, dass vor allem die quasi-rhythmische, oszillatorische Aktivität im Theta-Frequenzband (4–8 Hz) funktional mit sprachspezifischen und auch allgemeinen kognitiven Prozessen zusammenhängt (z.B., Meyer, 2017). Allerdings blieb zu untersuchen, ob Theta-Oszillationen auch im Ruhezustand eine funktionale Relevanz für sprachspezifische und allgemeine kognitive Prozesse haben. Darüber hinaus war bisher nicht geklärt, ob sich diese Netzwerke mit dem Alter verändern und ob sich solche Veränderungen auf das Verstehen von Sprache im Alter auswirken. Um diese offenen Fragen zu beantworten, wurde in der vorliegenden Arbeit der Zusammenhang zwischen Theta-Oszillationen im Ruhezustand und dem Satzverstehen über die Lebensspanne untersucht. Dazu wurden zunächst Elektroenzephalogramme (EEG) aufgenommen. Anschließend wurden mit Hilfe von Verhaltensexperimenten sprachspezifische und allgemeine kognitive Prozesse in Erwachsenen jüngeren, mittleren und älteren Alters (Durchschnittsalter: 25, 43, 65 Jahre) untersucht. Die Ergebnisse zeigten, dass Theta-Oszillationen im ruhenden Sprachnetzwerk unabhängig vom Alter mit dem Satzverstehen zusammenhängen. Schwierigkeiten im Satzverstehen zeigten einen signifikanten Zusammenhang mit einer Abnahme der oszillatorischen Aktivität im Theta-Frequenzband. Dieser Zusammenhang war in demjenigen Ruhenetzwerk zu beobachten, das sonst für Arbeitsgedächtnisprozesse relevant ist. Daher zeigen die Ergebnisse, dass das Satzverstehen durch zwei unterschiedliche Ruhenetzwerke unterstützt wird, aber dass nur dasjenige Netzwerk, das für das Arbeitsgedächtnis relevant ist, mit den Verständnisschwierigkeiten älterer Erwachsener zusammenhängt. Dieser Befund lässt vermuten, dass altersbedingte Veränderungen der Elektrophysiologie des ruhenden Gehirns das Satzverstehen beeinträchtigt.

In der zweiten Studie wurde näher auf die Schlüsselrolle des Arbeitsgedächtnisses für das Sprachverstehen im Alter eingegangen (Beese et al., eingereicht). Diese Studie baut auf der Idee auf, dass Sprache nur dann richtig verstanden werden kann, wenn sprachliche Informationen auch in das Arbeitsgedächtnis enkodiert werden. Das heißt, Schwierigkeiten mit dem Sprachverstehen könnten im Alter auftreten, sobald die Kapazität des Arbeitsgedächtnisses nicht mehr ausreicht, um alle sprachlichen Informationen zu enkodieren. Dazu wurde das EEG von erwachsenen Versuchspersonen jüngeren, mittleren und älteren Alters (Durchschnittsalter: 24, 43, 65 Jahre) aufgezeichnet, während sich die Versuchspersonen lange Sätze anhörten und sich die Satzinformationen für anschließende Verständnisfragen einprägten. Die Genauigkeit der Antworten wurde als Indikator für den Enkodierungserfolg verwendet. Der Unterschied in der oszillatorischen Aktivität zwischen richtig und falsch enkodierten Sätzen wurde in Form des subsequent memory effect (SME) zwischen den Altersgruppen verglichen. Altersunterschiede im SME konnten im Alphaband (8–10 Hz) gefunden werden. Dabei war der Enkodierungserfolg bei jüngeren Erwachsenen durch eine Abnahme oszillatorischer Aktivität gekennzeichnet. Sie zeigten geringere Aktivität bei richtig enkodierten Sätzen als bei falsch enkodierten Sätzen. Bei älteren Erwachsenen dagegen war der Enkodierungserfolg durch eine Aktivitätszunahme gekennzeichnet. Sie zeigten eine höhere Aktivität bei richtig enkodierten Sätzen als bei falsch enkodierten Sätzen. Da Alpha-Oszillationen oftmals mit inhibitorischen Prozessen in Verbindung gebracht werden, könnte es sein, dass der Enkodierungserfolg bei älteren Erwachsenen mit der Inhibitionsfähigkeit zusammenhängt. Es könnte sein, dass ältere Erwachsene das Enkodieren von detailierten Informationen inhibieren, um ihre geringe Arbeitsgedächtniskapazität nicht zu überlasten. Dadurch würden ältere Erwachsene möglicherweise weniger detaillierte Informationen extrahieren und könnten sich stattdessen auf die Kerninformation von Sätzen konzentrieren. Diese Ergebnisse untermauern die bedeutende Rolle des allgemeinen kognitiven Abbaus im Alter für das Satzverstehen.

In der dritten Studie wurde untersucht, ob die nachteiligen Auswirkungen des neurokognitiven Alterns für das Satzverstehen abgeschwächt werden können, indem die Informationsmenge durch sprachspezifische Prozesse reduziert wird (Beese et al., 2019). Ob sich jüngere und ältere Erwachsene diese sprachspezifische Informationen zu gleichem Maße zu Nutzen machen, um das Arbeitsgedächtnis zu entlasten, war die Frage der dritten Studie der hier vorliegenden Arbeit. Semantische und syntaktische Informationen können genutzt werden, um Relationen zwischen Worten herzustellen und einzelne Wörter zu Wortgruppen zusammenzufassen, so dass das Arbeitsgedächtnis entlastet wird. Zum Beispiel ist es möglich, auf der Basis von syntaktischen Informationen den Artikel „das“ mit dem Nomen „Boot“ zu der Nominalphrase „das Boot“ zu verbinden. Dabei werden also zwei syntaktische Repräsentationen zu einer syntaktischen Repräsentation zusammengefasst, was die Informationsmenge reduziert. Ganz ähnlich können auf der Basis von semantischen Informationen das Adjektiv „blau“ und das Nomen „Boot“ zu „blaues Boot“ verbunden werden. Dabei werden zwei semantische Repräsentationen zu einer semantischen Repräsentation zusammengefasst, was wiederum die Informationsmenge reduziert. In dem hier vorliegenden Experiment haben jüngere und ältere Erwachsene (Durchschnittsalter: 26 und 65 Jahre) Sätze (mit syntaktischen Informationen) und Wortlisten (ohne syntaktischen Informationen) gelesen, die jeweils aus realen Wörtern (mit semantischen Informationen) oder Pseudowörtern (ohne semantischen Informationen) bestanden. Anschließend wurden Fragen zur Wortfolge gestellt. Zwei Experimente wurden durchgeführt, um die Belastung des Arbeitsgedächtnisses zu variieren. Während die Sequenzen in Experiment 1 acht (Pseudo-) Wörter umfassten, wurde die Anzahl der (Pseudo-) Wörter in Experiment 2 auf elf erhöht. Die Ergebnisse zeigten, dass ältere Erwachsene weniger als jüngere Erwachsene von syntaktischen Informationen profitierten. Jedoch war der Nutzen semantischer Informationen bei beiden Altersgruppen vergleichbar. Möglicherweise können ältere Erwachsene die Vielfalt syntaktischer Details in Anbetracht ihrer reduzierten Arbeitsgedächtniskapazität nicht mehr nutzen und konzentrieren sich stattdessen auf die Kernaussagen eines Satzes. Das heißt, ältere Erwachsene fokussieren sich darauf, was gesagt wurde (die semantischen Informationen), aber weniger darauf, in welcher Form etwas gesagt wurde (die syntaktischen Informationen). Das könnte auf eine Verlagerung des Fokus von semantischen auf syntaktische Informationen in der Satzverarbeitung mit dem Alter hinweisen.

Insgesamt zeigen die Ergebnisse der hier vorliegenden Arbeit, dass das Sprachverstehen im Alter vom sprachspezifischen und allgemeinen kognitiven Abbau betroffen ist. Insbesondere konnte sowohl im Ruhezustand als auch während der Satzverarbeitung gezeigt werden, dass Schwierigkeiten mit dem Satzverstehen bei älteren Erwachsenen mit Veränderungen des elektrophysiologischen Netzwerks zusammenhängt, das für allgemeine kognitive Funktionen, wie das Arbeitsgedächtnis, relevant ist. Das bedeutet, dass sich sowohl die elektrophysiologischen Voraussetzungen, als auch die elektrophysiologischen Korrelate, die dem Satzverstehen zu Grunde liegen, mit dem Alter verändern. Dabei spielte vor allem das Enkodieren von Sätzen in das Arbeitsgedächtnis für das Satzverstehen eine große Rolle. Im Besonderen konnte gezeigt werden, dass es für das Satzverstehen bei älteren Erwachsenen wichtig ist, das Enkodieren von detaillierten Informationen zu inhibieren, vermutlich um eine Überlastung der ohnehin geringen Arbeitsgedächtniskapazität zu vermeiden. Eine Überlastung könnte damit zusammenhängen, dass sich die Verarbeitungskosten des Enkodierens erhöhen, wenn die gerade enkodierten Informationen von den vorher enkodierten Informationen beeinträchtigt werden (z.B., Lewis et al., 2006). Vorherige Studien haben gezeigt, dass eine solche Enkodierungsinterferenz beim Satzverstehen einen bedeutenden Einfluss hat (z.B., Gordon et al., 2002; Lewis & Vasishth, 2005; Lewis et al., 2006). Jedoch nimmt die Fähigkeit, Interferenzen zu inhibieren, im Alter ab. Daher kann es sein, dass ältere Erwachsene Schwierigkeiten haben, das Enkodieren detaillierter Informationen zu inhibieren, obwohl dies zu größeren Erfolgschancen beim Satzverstehen führen könnte. Nichtsdestotrotz gelingt es älteren Erwachsenen meist, Kernaussagen zu verstehen (z.B., Reder et al., 1986; Tun et al., 1998). Möglicherweise wird dies auch darin wiedergespiegelt, dass semantische Informationen über die Lebensspanne hinweg ähnlich für das Sprachverstehen genutzt werden können, während ältere Erwachsene weniger von detaillierten, syntaktischen Informationen profitieren als jüngere Erwachsene. Wenn das Enkodieren syntaktischer Informationen inhibiert ist, extrahieren ältere Erwachsene weniger syntaktische Details und fassen daher einzelne Worte nicht effektiv zu Wortgruppen zusammen, so dass das Arbeitsgedächtnis nicht entlastet werden kann. Dies erhöht den Verarbeitungsaufwand und ruft dann möglicherweise Schwierigkeiten mit dem Satzverstehen hervor. Daher fokussieren sich ältere Erwachsene womöglich eher darauf, was gesagt wurde (die semantischen Informationen), als darauf, in welcher Form etwas gesagt wurde (die syntaktischen Informationen). Insgesamt zeigen die Ergebnisse der hier vorliegenden Arbeit, dass das Satzverstehen im Alter von sprachspezifischen und allgemeinen neurokognitiven Abbauprozessen beeinflusst wird. Weitere Studien sind jedoch nötig, um den hier vorgeschlagenen Zusammenhang zwischen dem Enkodieren, der Inhibition und der Extraktion von unterschiedlichen sprachspezifischen Informationen zu bestätigen.

Curriculum Vitae

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List of Publications

in submission	Vassileiou, B., **Beese, C.**, Friederici, A. D., & Meyer, L. (in submission). Interaction of white-matter connectivity and oscillatory desynchronization explains
submitted	**Beese, C.**, Vassileiou, B., Friederici, A. D., & Meyer, L. (submitted). Age Differences in Encoding-Related Alpha Power Reflect Sentence Comprehension Difficulties
published	**Beese, C.**, Werkle-Bergner, M., Lindenberger, U., Friederici, A. D. & Meyer, L. (2019). Adult age differences in the benefit of syntactic and semantic constraints for sentence processing. Psychology and Aging, 34(1): 43-55
	Vassileiou, B., Meyer, L., **Beese, C.** & Friederici, A.D. (2018). Alignment of alpha-band desynchronization with syntactic structure predicts successful sentence comprehension. NeuroImage, 175: 286-296
	Beese, C., Meyer, L., Vassileiou, B. & Friederici, A.D. (2017). Temporally and spatially distinct theta oscillations dissociate a language-specific from a domain-general processing mechanism across the age trajectory. Scientific Reports, 7, 11202

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Selbständigkeitserklärung

Hiermit bestätige ich, Caroline Beese, die hier vorliegende Arbeit mit dem Titel „The Effects of Neurocognitive Aging on Sentence Processing“ selbstständig verfasst zu haben. Andere Werke und Quellen, auf die ich mich beziehe, habe ich kenntlich gemacht. Ich habe keine anderen Hilfsmittel, als die angegebenen, verwendet.

Hereby I, Caroline Beese, confirm that this thesis entitled “The Effects of Neurocognitive Aging on Sentence Processing” is my own original work. Auxiliary sources and work of others that I used have been acknowledged. I have not made use of any other resources or means than those indicated.

Leipzig, 18.04.2019

Caroline Beese

Nachweis über die Anteile der Co-Autoren

Nachweis über Anteile der Co-Autoren
Caroline Beese
The effects of neurocognitive aging on sentence processing

Nachweis über Anteile der Co-Autoren:

Titel: Temporally and spatially distinct theta oscillations dissociate a language-specific from a domain- general processing mechanism across the age trajectory

Journal: Scientific Reports

Autoren: Caroline Beese, Lars Meyer, Benedict Vassileiou & Angela D. Friederici

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Journal: Psychology and Aging

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