The role of neural feedback in language unification:

How awareness affects combinatorial processing

Valeria Mongelli

The role of neural feedback in language unification: How awareness affects combinatorial processing

PhD Thesis, Max Planck Institute for Psycholinguistics

ISBN: 978-94-92910-07-3

Cover artwork by Valeria Mongelli

Printed and bound by Ipskamp Drukkers bv

The role of neural feedback in language unification:

How awareness affects combinatorial processing

Proefschrift

ter verkrijging van de graad van doctor
aan de Radboud Universiteit Nijmegen
op gezag van de Rector Magnificus prof. dr. J.H.J.M. van Krieken,
volgens besluit van het college van decanen
in het openbaar te verdedigen op maandag 20 januari 2020
om 14.30 uur precies

door
Valeria Mongelli
geboren op 7 september 1990
te Bari, Italië

Promotor:

Prof. dr. Peter Hagoort

Copromotor:

Dr. Simon van Gaal (Universiteit van Amsterdam)

Manuscriptcommissie:

Prof. dr. Floris P. de Lange

Prof. dr. Laurent Cohen (Sorbonne Universiteit, Frankrijk)

Dr. Marte Otten (Universiteit van Amsterdam)

The role of neural feedback in language unification:

How awareness affects combinatorial processing

Doctoral thesis

to obtain the degree of doctor
from Radboud University Nijmegen
on the authority of the Rector Magnificus prof. dr. J.H.J.M. van Krieken,
according to the decision of the Council of Deans
to be defended in public on Monday, January 20, 2020
at 14.30 hours

by
Valeria Mongelli
born on September 7, 1990
in Bari (Italy)

Supervisor:

Prof. dr. Peter Hagoort

Co-supervisor:

Dr. Simon van Gaal (Universiteit van Amsterdam)

Doctoral thesis committee:

Prof. dr. Floris P. de Lange

Prof. dr. Laurent Cohen (Sorbonne University, France)

Dr. Marte Otten (University of Amsterdam)

To my grandmother

Table of contents

1

General introduction

A sentence uttered makes a world appear
Where all things happen as it says they do […]
W. H. Auden

1.1. Introduction

Most living creatures have a code of communication. Still, human communication code uniquely differs from that of any other living entity. Why? While most animals communicate continuously and effortlessly, human communication faculty, which we call language, is the only faculty that is virtually infinite in its capacity of expression. Humans are able to create entire worlds with words. How come? The ability of the human brain to flexibly combine a finite amount of words into an infinite set of sentences is a crucial, still unanswered issue.

Language is a high-level cognitive faculty, and as such it relies on many low-level faculties like audition, vision and memory. Accordingly, the language network is distributed within the brain, and engages multiple areas specialized in different subcomponents. The way these areas interact to generate language is not well understood.

Within language processing, one can distinguish between single word and sentence processing. As most neuroscience research in the last decades focused on the single word level, little is known on how the brain processes language at the sentence level. Developing a neurobiologically plausible account of language processing beyond single words remains one of the foundational challenges for cognitive neuroscience. In the course of my thesis, I investigated which brain mechanisms allow us to disentangle sentence and single word processing.

1.2. The Memory, Unification and Control (MUC) model

How is language implemented in the brain? The Memory, Unification and Control (MUC) model (Hagoort, 2005, 2013, 2017) aims to provide a neurobiologically plausible account of the language faculty, both at the sentence and single word level. First, the MUC model intends to overcome the classical Wernicke-Lichtheim-Geschwind (WLG) model (**Figure 1.1**). According to this traditional framework, the language network is located in the perisylvian cortex. Within the perisylvian cortex, the main anatomical components are Broca's area in the left inferior frontal cortex (LIFC) and Wernicke's area in the left superior temporal cortex, connected by the arcuate fasciculus. Broca's and Wernicke's areas are responsible for language production and comprehension, respectively. Although this traditional model still has a certain impact, it is now considered as too simplistic

(Hagoort, 2005; Hickok & Poeppel, 2007). Indeed, it does not accurately describe all processes that take place within the brain during language comprehension.

During language comprehension, we process the input incrementally. When we read or listen to a sentence, we retrieve from long-term memory the meaning and syntactic properties of the words that are part of the utterance. This lexical information has to be maintained in short-term memory while we perceive the following words, in order to combine all word pieces in a coherent interpretation of the whole utterance. In parallel, other processes, e.g. attention or prediction processes, take place, so that based on the context (i.e. earlier words in the sentence) we are able to constrain our expectations of what the next word will be.

Within the MUC framework, language processing is divided among three main components: Memory, Unification and Control (Hagoort, 2005). The Memory component refers to the lexical retrieval of the linguistic information stored in long-term memory. This information includes the word’s form, its syntactic properties and its meaning (in psycholinguistic terms, this is defined as the mental lexicon – cf. for example Levelt, 1992). The Unification component refers to the combination of words into multiword utterances and sentences. Note that, in this work, we will employ the terms “unification”, “combinatorial processing” and “sentence processing” as synonyms. The Control component is responsible for the executive control operations that are involved in selecting the right language, or in turn-taking during a conversation, etc. This tripartite distinction applies to both language production and comprehension, and to both the visual and auditory domains.

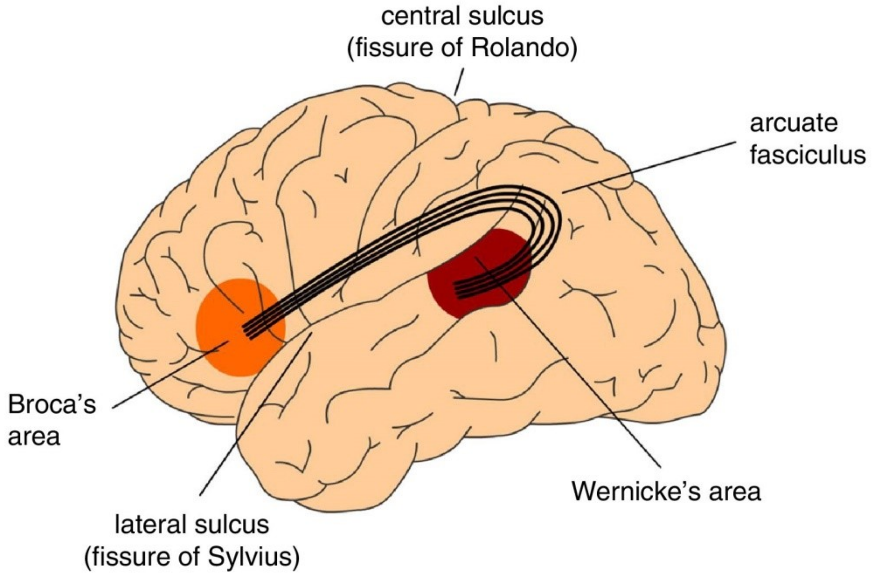

Figure 1.1: The classical Wernicke-Lichtheim-Geschwind (WLG) language model. Language network is located in the perisylvian cortex. Within the perisylvian cortex, the main anatomical components are Broca's area in the left inferior frontal cortex (LIFC) and Wernicke's area in the left superior temporal cortex (LSTC), connected by the arcuate fasciculus. Broca's and Wernicke's area are responsible for language production and comprehension, respectively. Reprinted with permission from Hagoort (2014).

1.2.1. Semantic unification

Semantic unification is defined as "the integration of word meaning into an unfolding representation of the preceding context" (Hagoort, Baggio, & Willems, 2009). This definition points to the expressive power of language, and to the fact that the meaning of a sentence (or of a multiple-word utterance) is more than the mere concatenation of single word meanings. Consider, for example, the expressions *flat beer*, *flat note* and *flat tire*[1]: the adjective *flat* is semantically ambiguous, as it conveys very different meanings across the three utterances. Taking this into account, studies on semantic unification usually compare either sentences with and without semantic ambiguities, or sentences with and without semantic anomalies[2]. The assumption behind this approach is that ambiguous (or anomalous) sentences should increase the processing load, and therefore the activation, of brain areas devoted to semantic processing.

Evidence from functional magnetic resonance imaging (fMRI) literature describes the semantic unification network as including (at least) the left inferior frontal, left superior/middle temporal, and left inferior parietal cortex and, to a lesser extent, their right-hemispheric homologues (Davis et al., 2007; Friederici, Rueschemeyer, Hahne, & Fiebach, 2003; Kiehl, Laurens, & Liddle, 2002; Rodd, Davis, & Johnsrude, 2005; Snijders et al., 2009; Willems, Özyürek, & Hagoort, 2007). Within this network, the LIFC is thought to subserve semantic unification, while the left posterior temporal cortex (LPTC) is more involved in the retrieval of lexical-semantic information (single word processing) (Hagoort, 2017; Willems et al., 2007).

1.2.2. Syntactic unification

Syntactic unification refers to the combination of lexical items (words or chunks of structures, e.g. adjective+noun) retrieved from memory into larger

---

[1] Example taken from Keenan (1979) and cited by Hagoort et al. (2009) and Hagoort (2017).

[2] Example of semantically plausible vs. anomalous sentence: "The shirt was ironed" vs. "The thunderstorm was ironed" (taken from Friederici et al., 2003).

structures (e.g. noun or verb phrases). This implies checking that agreement features (e.g. number, gender, person) of different lexical items match with each other.

Following the same logic of semantic unification studies, work on syntactic unification compared syntactically ambiguous and non-ambiguous sentences. For example, in an fMRI study by Snijders et al. (2009), participants read sentences and strings of words containing word category (noun-verb) ambiguous words (e.g. *copy*) at critical positions, i.e. in a position in which it may be interpreted as either a noun or a verb (Snijders et al., 2009). The LIFC showed enhanced activation for sentences compared to words, and within sentences increased activation for ambiguous compared to unambiguous conditions. The LPTC was more activated for ambiguous than unambiguous conditions, in both sentence and strings of word sequences. This was interpreted as evidence for a distribution of labor between LIFC and LPTC for syntactic unification and lexical retrieval, respectively.

1.2.3. The interplay between semantic and syntactic unification

In a large meta-analysis of studies on sentence processing, Hagoort & Indefrey (2014) found that the LIFC is the region most reliably activated during unification operations (Hagoort & Indefrey, 2014). Within this region, there may be a gradient for semantic and syntactic operations. Indeed, syntactic unification relies on more dorsal parts of the LIFG (BA 44/45), whereas semantic unification activates more ventral parts (BA 45/47). Syntactic and semantic networks are partially overlapping, which fits with the idea that syntactic and semantic unification processes cannot be fully separated and should, therefore, be investigated separately.

Overall, fMRI (e.g. Snijders et al., 2009), connectivity (Catani et al., 2007; Xiang, Fonteijn, Norris, & Hagoort, 2010) and lesion studies (Tyler et al., 2011) suggest that LIFC plays a crucial role in language unification. However, given their scarce temporal resolution, hemodynamic and diffusion techniques cannot fully account for the speed at which language occurs. Electrophysiological measurements[3], having much higher temporal resolution, add crucial insights to a plausible functional interpretation of the language network.

---

[3] Typical electrophysiological techniques are electroencephalography (EEG), which records event related potentials (ERPs) and magnetoencephalography (MEG), which records event related fields (ERFs).

1.3. The role of feedback processing in language unification

Language comprehension is an incredibly fast process. Even if pronouncing a few words can take hundreds of milliseconds, the first language-related electrophysiological signal (i.e. the ELAN, see **Box 1**) already occurs 100-150 ms after word onset. Therefore, it is thought that first language processes are only mediated by feedforward connections, which involve spread of activation from low-level to high-level areas and proceed very rapidly. On the contrary, later language processes may also rely on slower, re-entrant feedback connections (Hagoort, 2017). Accordingly, only late language-related ERP effects (e.g. the P600, cf. **Box 1**) are thought to rely on feedback connections. The case of the N400 (cf. **Box 1**) is controversial. On the one hand, the N400 may rely on feedback processing, since responses occurring later than 200 ms are thought to be mediated by feedback connections (Garrido, Kilner, Kiebel, & Friston, 2007). On the other hand, the onset of the N400 follows the onset of word recognition closely in time (Hagoort, 2017), which suggests that the N400 effect is partially based on predictive processing, and potentially on feedforward connections[4].

When we read (or hear) a sentence, the cascade of feedforward connections (feedforward sweep) proceeds from early sensory areas (pre-lexical processing) to temporal cortex, where memory retrieval and semantic interpretation of single words occur (Salmelin, 2007). Unification processes involve higher-level semantic areas for combinatorial processes that, as explained above, probably include the LIFC. According to the MUC framework, after the signal from temporal cortex reaches the LIFC, frontal neurons send the signal back to adjacent regions within temporal cortex (**Figure 1.2**). Thanks to feedback processing from LIFC to temporal regions, lexical information is actively maintained, which is crucial for combining words into a sentence over time. For this reason, long-range feedback processing is hypothesized as crucial for language unification (Hagoort, 2017), in contrast with purely feedforward language models (e.g. Cutler & Clifton, 1999).

Evidence for this claim was found by a recent magnetoencephalography (MEG) study by Hultén and colleagues, who investigated the correlation between distant cortical areas during word-by-word sentence reading by means of inter-areal co-modulation within an individual (Hultén, Schoffelen, Uddén, Lam, & Hagoort, 2019). They found a co-modulation between LIFC and LPTC occurring 400 ms after the onset of each word, across the progression of a sentence. In a previous study, the authors showed that posterior temporal and frontal regions display bidirectional Granger Causal interactions in direction-specific frequency bands (Schoffelen et al., 2017). Taken together, these results suggest that language uni-

---

[4] For a more extensive analysis of the nature of the N400 effect, cf. **Box 2**.

fication is realized in a dynamic interplay between LIFC and LPTC. However, it remains unknown whether feedback from LIFC to LPTC is necessarily required for language unification, as predicted by the MUC model.

In the course of my thesis, I explored the role of feedback processing in unification and lexical retrieval, as a small window into the organization of the language network. To approach this question, I investigated which language processes are preserved when disrupting long-range feedback connections by means of visual masking. Therefore, I now turn to review existing evidence on visual masking and the effects of such a technique.

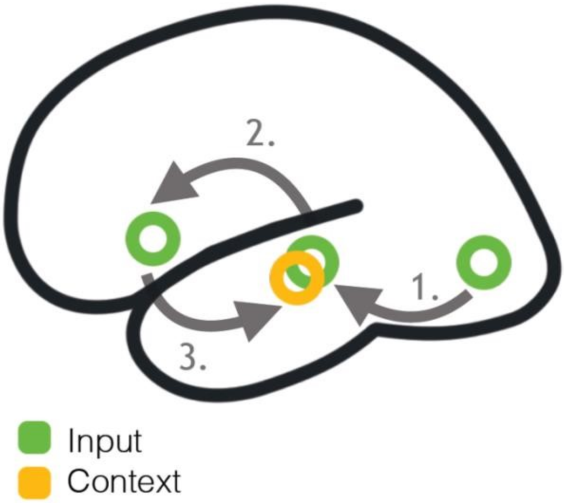

Figure 1.2: Schematic overview of language unification processes within the left hemisphere. During sentence comprehension, the input proceeds from early sensory areas (pre-lexical treatment) to temporal cortex (arrow 1), where it is processed at the lexical level. Next, the input is sent to left inferior frontal areas (arrow 2), which subserve unification mechanisms. Finally, frontal neurons send the signal back to temporal regions from which forward input originated (arrow 3). Thanks to feedback processing from frontal to temporal regions, context is created and lexical information is actively maintained, which is crucial for combining words into a sentence over time. Figure adapted from Hagoort (2017). Graphical re-adaptation: René Terporten.

Box 1: ERP markers of language processing

Early Left Anterior Negativity/Left Anterior Negativity (ELAN/LAN)

The ELAN (or LAN, depending of its latency of occurrence) is a frontally distributed negative event-related potential (ERP), usually left-lateralized (Friederici et al., 1993). Its latency ranges between 150 and 400 ms. ELAN/LAN has been associated with - among others - morphological (e.g. **The parquet was polish*) and syntactic (e.g. **The friend was in the visited*) violations. Note that in linguistics, the star is used to mark an utterance considered as ungrammatical.

N400

N400 is a negative ERP deflection, starting around 250 ms after the onset of the critical word, with a peak around 400 ms. It was first described as a difference in amplitude between sentences with a semantic anomalous ending (e.g. *I drink socks*), compared to semantically plausible sentences (e.g. *I drink coffee*) (Kutas & Hillyard, 1980). Since then, N400 has been extensively studied and it is now associated with a broad range of linguistic and non-linguistic phenomena (Kutas & Federmeier, 2010; Lau et al., 2008). A paradigm that is typically employed to study the N400 effect is semantic priming. Semantic priming is the phenomenon for which when a target word, e.g. *cat*, is preceded by a related prime word, e.g. *dog*, this results in shorter reaction times (RTs) and less response errors compared to an unrelated word (e.g. *lamp*). On the neural level, unrelated prime-target pairs trigger a larger N400 than related pairs.

P600

P600 is a centroparietal distributed positivity, usually peaking around 600 ms (Hagoort et al., 1993; Osterhaut & Holcomb, 1992). It has been associated with morphological and syntactic violations (cf. examples above), and more complex syntactic processes of reanalysis and repair, for example in response to the so-called garden path sentences (i.e. sentences in which, at critical points, the reader has to revise the structure initially followed – e.g. *The horse raced past the barn fell*).

ERP effect vs. ERP component

In the context of this work, it is worth noticing the difference between ERP component and ERP effect. For example, the N400 component is evoked by every content word, independently of the sensory modality in which it is presented. The N400 effect is the difference in amplitude between the N400 components evoked by two words in two different experimental conditions (e.g. anomalous vs. plausible, as in the seminal study by Kutas & Hillyard 1980). For the difference between N400 component and N400 effect, cf. Baggio & Hagoort (2011).

Box 2: The nature of the N400 effect

Two opposing theories aim to explain the N400 effect: the integration theory and the lexical theory (Kutas & Federmeier, 2010; Lau et al., 2008). Within the integration theory, the N400 effect results from semantic integration of the critical word within the current context. Accordingly, the N400 effect is combinatorial, that is reflects post-lexical, controlled processes (Baggio & Hagoort, 2011. For the difference between automatic and controlled memory processes, cf. Shiffrin & Schneider, 1977). This view is supported by the observation that the N400 effect occurs too late to reflect lexical access, and explains the N400 effect being larger in semantically anomalous, compared to plausible sentences (Kutas & Hillyard, 1980): when expectations are not attended, integration is more costly. The same logic holds for semantic priming studies. According to the integration theory, the N400 effect reflects the degree of difficulty of integrating a word with the preceding context, where context can be a single word or a whole sentence.

Within the lexical theory, the N400 is a non-combinatorial, automatic effect, reflecting lexical access (Deacon, Dynowska, Ritter, & Grose-Fifer, 2004). Given that every lexical item is linked to a long-term memory representation, the N400 effect reflects the facilitated activation of features of this representation. Accordingly, the difference between anomalous and plausible sentences (or related vs. unrelated prime-target pairs) is due to easier memory access of predictable, compared to unpredictable words.

Overall, evidence in favor of one theory or the other is mixed (Baggio & Hagoort, 2011; Kutas & Federmeier, 2010; Lau et al., 2008). Since the N400 effect is driven by many different factors, and reflects a considerable amount of language and memory-related processes, the integration/lexical dichotomy may also be too simplistic. A revised theoretical account of the N400 effect should aim to provide a coherent explanation of these mixed findings.

1.5. Reducing visual awareness: Historical and empirical background of research on masked processing

Visual masking is one technique to manipulate the level of conscious access to sensory inputs (cf. **Box 3**). Since the beginning of 20th century, visual masking has been employed to investigate unconscious processing (Breitmeyer & Ogmen, 2000). Masking is known to significantly reduce stimulus awareness, even if the extent to which awareness is reduced (i.e. absent or partially absent awareness) is debated and depends on several experimental factors (e.g. masking strength, task settings, etc.) (Kouider & Dehaene, 2007).

Since the pioneering work of Anthony Marcel (Marcel, 1980), masking has been used to study the possibility of language to be treated outside of conscious perception. One of the main methods to investigate this issue is masked semantic priming. In a typical masked priming paradigm, related prime-target pairs (e.g. *cat-dog*) are compared to unrelated pairs (e.g. *cat-lamp*), as in traditional semantic priming[5]. However, in this case the prime is masked from awareness by a backward mask and/or a forward mask. This masked condition is usually compared with an unmasked condition, in which both prime and target are fully visible. When fully invisible, masked primes are also defined as “unconscious” or “subliminal”.

There is a considerable amount of work showing that masked primes trigger behavioral and neural signatures of semantic processing, similarly to fully visible primes (for an extensive review, cf. Kouider & Dehaene, 2007). On the neural level, it has been found that unrelated masked prime-target pairs trigger a larger N400 effect than related pairs (Kiefer, 2002). Masked syntactic priming[6] has been much less investigated. There are only a few studies finding behavioral (Berkovitch & Dehaene, 2019) and neural (Iijima & Sakai, 2014) effects of masked syntactic processing.

It should be noted that masked semantic and syntactic priming effects have not always been replicated (Batterink, Karns, Yamada, & Neville, 2010; Brown & Hagoort, 1993). In general, masked priming effects are weak, short-lived and much smaller compared to fully visible conditions. Moreover, they are strongly affected by experimental and task settings (Kouider & Dehaene, 2007; Van den Bussche, Van den Noortgate, & Reynvoet, 2009).

Research on masked semantic/syntactic priming cited above has mostly been done on single word processing. There is a recent body of work exploring the lim-

---

[5] For an explanation of traditional semantic priming cf. **Box 1**.

[6] As an example, syntactic priming can be induced by words of the same grammatical category (e.g. Noun-Noun), compared to words of different categories (e.g. Noun-Verb).

its of language processing under reduced levels of awareness, and results are mixed (for a comment, cf. Rohaut & Naccache, 2018). It has been found that masked priming effects may occur for multiple words (Armstrong & Dienes, 2013; van Gaal et al., 2014), and even for entire sentences (Armstrong & Dienes, 2014; Nakamura et al., 2018; Sklar et al., 2012). However, effects are strongly dependent on experimental factors such as subjects' training (van Gaal et al., 2014). Moreover, some of these results failed replication (Rabagliati, Robertson, & Carmel, 2018; Yang, Tien, Yang, & Yeh, 2017)[7].

So far, I have explained how visual masking is employed to reduce stimulus awareness. This leaves unanswered the question of how masking affects brain mechanisms of visual processing, to which I now turn.

1.6. Visual masking disrupts feedback processing in the brain

There are a number of theories that aim to explain the mysteries of consciousness, both at the theoretical and the empirical level. Among those, the Global Workspace Theory (GWT, Baars, 1988; Dehaene & Changeux, 2011), the Integrated Information Theory (IIT, Tononi & Koch, 2008), and the Recurrent Processing Theory (Lamme, 2006) are some of the dominant frameworks. These theories obviously differ on many aspects, but agree on the fact that conscious experience relies on a more extended, integrated and complex brain network compared to unconscious experience.

When a stimulus is consciously perceived, there is intense activation extending to high-level areas (parieto-frontal network), and information can be durably maintained in working memory (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). Recurrent processing is established between high-level and low-level areas (Lamme, 2006). On the contrary, when a stimulus does not reach conscious access, activation is weak and only confined to posterior sensory areas. Local recurrent processing between low-level areas may be present, but only when the bottom-up input is strong enough (preconscious processing, Dehaene et al., 2006). In this case, the stimulus may reach high-level areas, but only in a feedforward sweep (Lamme, 2006).

---

[7] Only the study by Rabagliati et al. (2018) is a direct failed replication of Sklar et al. (2012). The study by Yang et al. (2017) independently showed missing evidence for unconscious sentence processing. Moreover, note that these studies employed different masking techniques. Van Gaal et al. (2014), Nakamura et al. (2018), Armstrong & Dienes (2013) and Armstrong & Dienes (2014) employed visual masking, while Sklar et al. (2012), Rabagliati et al. (2018) and Yang et al. (2017) employed continuous flash suppression (CFS). For an explanation of visual masking and CFS, see **Box 3**.

Box 3: Methods to study consciousness

In decades of scientific work on consciousness, neuroscientists have employed many techniques to experimentally manipulate the level of conscious access to sensory inputs. Here, I only mention the techniques that are relevant in the context of this thesis.

Visual masking

In a visual masking experiment, a target image is preceded and followed (or in the case of backward masking, only followed) closely in time by a mask. The mask can be a flash of light, an image sharing many structural features with the target, random-dot noise, strings of letters and/or symbols (Breitmeyer & Ogmen, 2000). The target presenting time is very short, usually between 16 and 20 ms. The mask has a longer presenting time, which varies from 50 ms up to hundreds of milliseconds. The time from mask onset to target onset can be experimentally manipulated, and is defined as stimulus onset asynchrony (SOA).

Continuous Flash Suppression (CFS)

This masking technique (Tsuchiya & Koch, 2005) works by continuously flashing different images rapidly into one eye, while the input to the corresponding location in the other eye remains the same. This method has the advantage that stimuli can be presented for a longer time compared to visual masking. However, CFS has been criticized, and it is currently debated whether it can be considered as a valid technique to compare conscious and unconscious stimuli (Stein et al., 2011).

Attentional Blink (AB)

A typical AB paradigm (Raymond, Shapiro, & Arnell, 1992) employs Rapid Serial Visual Presentation (RSVP), in which two targets are presented within a fast visual stream of other stimuli (e.g. letters, pictures or digits). The visual consciousness of the second target is diminished, due to attentional capture of the first target.

Direct vs. Indirect measures of consciousness

Measures of perception without consciousness usually rely on the dissociation between two indices of perceptual processing (Reingold & Merikle, 1988). One index indicates the availability of stimulus information to consciousness (direct measure, e.g. discrimination trials), while the other indicates the availability of stimulus information independently of consciousness (indirect measure, e.g. ERPs or RTs). Evidence of information processing requires that stimulus information unavailable to consciousness, as indicated by direct measures (in which performance is at chance level), is still perceived and capable of influencing perceptual, cognitive and semantic processes, as indicated by indirect measures (in which performance is above chance level).

Previous research on visual perception showed that masking interferes with visual awareness by disrupting feedback processing from higher to lower visual areas, whereas feedforward processing is substantially preserved (Fahrenfort, Scholte, & Lamme, 2007; Fahrenfort, van Leeuwen, Olivers, & Hogendoorn, 2017; Kovacs, Vogels, Orban, & Sprague, 1995). Other studies showed that masking also disrupts long-distance feedback processing from frontal areas to higher visual areas (Del Cul, Dehaene, Reyes, Bravo, & Slachevsky, 2009). Taken together, these findings suggest that masking interferes with feedback processing between frontal and temporal areas, while leaving feedforward processing relatively intact.

1.7. Main research aim and thesis outline

In this thesis, I tested a crucial prediction of the MUC model, i.e. that feedback processing, likely involving frontal and temporal areas, is required for language unification (sentence processing), but not for lexical retrieval (single word processing). To this aim, I employed visual masking to disrupt feedback processing and investigated whether, under these conditions, unification processes were preserved. In a series of four experiments distributed across four experimental chapters, I investigated semantic and syntactic unification separately through four electroencephalography (EEG) experiments.

In Chapter 2 and 3, I asked whether feedback processing is necessary for semantic unification. In Chapter 2, I compared masked and unmasked processing of sequentially presented sentences and single words. Since I found that ERP neural signatures of semantic processing in the masked condition were short-lived, in Chapter 3 I compared simultaneously presented sentences and single words. In Chapter 4 and 5, I addressed the question whether feedback processing is necessary for syntactic unification. In Chapter 4, I found task-related effects on both masked and unmasked unification and lexical retrieval processes. I conducted a follow-up experiment, reported in Chapter 5, in order to further investigate these task-related effects. In Chapter 6, I discussed the main conclusions that can be drawn from this work, the implications for language and consciousness theories, and suggested directions for future research.

2

Is feedback processing necessary for semantic unification? How awareness affects sequentially presented sentences

This chapter appeared in: Mongelli, V., Meijs, E. L., van Gaal, S., & Hagoort, P. (2019). No language unification without neural feedback: How awareness affects sentence processing. *NeuroImage*, *202*, 1–12. (Experiment 1)

Abstract

How does the human brain combine a finite number of word meanings to form infinite sentences? According to the Memory, Unification and Control (MUC) model, semantic unification requires long-range feedback from the left inferior frontal cortex (LIFC) to left posterior temporal cortex (LPTC). Single word processing however may only require feedforward propagation of semantic information from sensory regions to LPTC. Here we tested the claim that long-range feedback is required for semantic unification by reducing visual awareness of words using a masking technique. Masking disrupts feedback processing while leaving feedforward processing relatively intact. Previous electroencephalography (EEG) studies have shown that masked single words still elicit an N400 effect, a neural signature of semantic incongruency. However, whether multiple words can be combined to form a sentence under reduced levels of awareness is controversial. To investigate this issue, we performed one EEG experiment in which 40 subjects performed a masked priming task. Words were presented sequentially, thereby forming a short sentence that could be congruent or incongruent with a target picture. This sentence condition was compared with a single word condition, in which either a noun (e.g. *man*) or a verb (e.g. *pushes*) was followed by congruent/incongruent pictures. Importantly, single words occurred in the first, second or third prime position. In the unmasked condition, ERPs time-locked to the picture onset showed a classical N400 effect for both sentences and single words. On the contrary, in the masked condition an N400 effect was only found for single words occurring just before picture onset (i.e. in the third prime position). Overall, our findings suggest that (i) semantic unification requires long-range feedback, at least when words are sequentially presented; and (ii) masked word processing is fleeting, i.e. dependent on stimulus onset asynchrony.

2.1. Introduction

Language processing involves single word and sentence processing. In both production and comprehension, single word processing is based on lexical retrieval from memory, whereas sentence processing also requires concatenation of retrieved lexical items and the combination of these items into novel meanings. Within the Memory, Unification and Control (MUC) model, the combinatorial aspect of language has been referred to as unification (Hagoort, 2005, 2013, 2017). Describing the neural network subserving unification, and what differentiates this network from related lexical retrieval mechanisms, is a major challenge in brain research (Dehaene, Meyniel, Wacongne, Wang, & Pallier, 2015; Hagoort, 2017). As described in the Introduction, unification takes place both at the semantic and the syntactic level. Semantic unification has been defined as "the integration of word meaning into an unfolding representation of the preceding context" (Hagoort et al., 2009).

There is some evidence for a distribution of labor between left posterior temporal and left inferior frontal regions for lexical retrieval and semantic unification, respectively (Snijders et al., 2009). According to the MUC model, lexical retrieval may be mainly dependent on feedforward propagation of semantic information from sensory regions to the left posterior temporal cortex (LPTC), whereas semantic unification is thought to require feedback from the left inferior frontal cortex (LIFC), which includes Broca's area, and the LPTC (Hagoort, 2013, 2017; Hultén et al., 2019; Schoffelen et al., 2017).

Here we tested the claim that feedback processing is required for semantic unification. To this aim, we reduced visual awareness of words using a visual masking technique. Although still a matter of investigation, it seems that masking may disrupt both local feedback mechanisms in visual cortex (Fahrenfort et al., 2007), as well as more long-range feedback mechanisms (e.g. from frontal cortex, Del Cul et al., 2009), while leaving feedforward processing relatively intact (Fahrenfort et al., 2007, 2017; Kovacs et al., 1995; Lamme & Roelfsema, 2000). Previous studies have shown that masked single words still trigger behavioral and neural signatures of semantic processing (see Kouider & Dehaene, 2007 for a review). For example, when a visible target (e.g. *cat*) is preceded by an unrelated masked prime (e.g. *bottle*), this results in longer reaction times and more response errors compared to prime-target pairs that are related (e.g. *dog-cat*) (Brown & Hagoort, 1993; Greenwald, Draine, & Abrams, 1996; Marcel, 1980). In electroencephalography (EEG), unrelated vs. related prime-target pairs trigger a larger N400 (Kiefer, 2002), a negative event-related potential (ERP) effect often associated with semantic violations (Kutas & Hillyard, 1980). However, whether semantic unification can also be achieved under reduced levels of awareness is highly controversial. There is evidence showing that simple combinatorial operations, like the negation of valence (e.g. *not good*), can be performed under masked processing (Armstrong & Dienes, 2013; van Gaal et al., 2014), although only after considerable training of the negation process (van Gaal et al., 2014). Some authors have suggested that semantic unification occurs for entire sentences (Armstrong & Dienes, 2013; Nakamura et al., 2018; Sklar et al., 2012), even though evidence is mixed (Rabagliati et al., 2018; Yang et al., 2017).

In this study, we tested the prediction that long-range feedback is necessary for semantic unification, but not (or less so) for lexical retrieval. We addressed this issue by interfering with neural feedback by means of visual masking and investigated whether, under these conditions, semantic unification could still occur. To this aim, we designed a new experimental paradigm carefully disentangling sentence and single word processes. Using EEG, we measured brain responses to sequentially presented masked and unmasked short sentences (e.g. *man-pushes-woman*). Sentences were followed by a picture, which was either congruent or incongruent with the previous sentence. This sentence condition was compared with a single word condition, in which either masked/unmasked nouns (e.g. *man*) or verbs (e.g. *pushes*) were followed by congruent/incongruent pictures. Importantly, single words could occur in the first, second or third prime position, i.e. at different stimulus onset asynchronies (SOAs)[8].

In the unmasked condition, for both sentences and single words, we expected an N400 effect. In the masked condition, we also expected an N400 effect for single words, replicating previous findings (Deacon, Hewitt, Yang, & Nagata, 2000; Kiefer, 2002; Kiefer & Brendel, 2006; Kiefer & Spitzer, 2000). For masked sentences, there were two possible scenarios. If masked sentences triggered an N400 effect, similarly to masked single words, this would suggest that feedback processing (likely from frontal to temporal regions) is not required for semantic unification. However, if no N400 effect was present for masked sentences, we may conclude that long-range feedback is required for semantic unification to occur.

2.2 Material and methods

2.2.1 Participants

44 subjects (34 females) participated in this study. 4 subjects did not complete the experiment, hence were excluded from the analyses. All subjects were right-handed native Dutch speakers, aged between 18 and 35, had normal or cor-

---

[8] SOA is the time from mask onset to target onset.

rected-to-normal vision, no neurological history and were naive to the purpose of the experiment. Subjects all gave written informed consent prior to participation, according to the Declaration of Helsinki. They received 36 euros for their participation.

2.2.2. Stimuli

In the sentence condition, we employed three-word sentences composed of an agent, an action and a patient (e.g. *man pushes woman*, in Dutch *man duwt vrouw*). Importantly, sentences were obtained by combining words that are not lexically related. The nouns employed to fill the agent/patient roles were the following: *man, woman, boy, girl* (in Dutch: *man, vrouw, jongen, meisje*). The verbs employed to fill the action role were the following: *pushes, measures, drags, finds* (in Dutch: *duwt, meet, sleept, vindt*). Sentences were presented sequentially, i.e. word by word. Each sentence was followed by a picture, either congruent or incongruent with the previous sentence (**Figure 2.1A**). Pictures were selected from a previously tested database (Menenti, Gierhan, Segaert, & Hagoort, 2011). They depicted transitive events such as *pushing* or *dragging* and the agent/patient of this action. Each picture included one male and one female actor (either adults or children), with one of the two actors (either the male or the female) playing the agent role. The position of the agent (left or right) was randomized. The database was tested by Menenti et al. (2011) to check whether the actions depicted in the pictures were clear. Then, the verb that was most commonly used to describe each action was selected to create the word-picture pairs.

In the noun and verb condition, we employed respectively the same four nouns and four verbs that were used in the sentence condition. Importantly, both nouns and verbs occurred in the first, second or third prime position. The other positions were filled by hashtags, e.g.: 1. *man #### ####*; 2. *#### man ####*; 3. *#### #### man*. In the noun condition, words were followed by a picture depicting a man, a woman, a boy or a girl. In the verb condition, pictures were the same as employed in the sentence condition. As in the sentence condition, pictures were either congruent or incongruent with the previous noun/verb. In all conditions, pictures were in greyscale and had a size of 400x300 pixels.

The masks consisted of seven randomly chosen uppercase letters, which were slightly overlapping to increase the density of the mask. The space between the center of each letter was 10 pixels. Words and masks were presented in Arial lowercase font with a size of 20. Linguistic stimuli were presented in white against a black background. Participants were seated at a distance of approximately 110 cm from the computer screen.

2.2.3. Experimental design

The experiment was programmed using Presentation software (Neurobehavioral Systems, Albany, NY, USA). We employed a 2 (primes semantic complexity: sentence or single word) x 2 (target congruency: congruent or incongruent) x 2 (masking strength: masked or unmasked) factorial design. In the sentence condition, incongruency was equally divided across three subcases: (1) incongruent actors/congruent action (e.g. sentence: *man pushes woman*, followed by a picture of a woman pushing a man); (2) congruent actors/incongruent action (e.g. *man pushes woman*, followed by a picture of a man measuring a woman); (3) incongruent actors/incongruent action (e.g. *man pushes woman*, followed by a picture of a woman measuring a man). Each sentence block included 112 trials and lasted approximately 5 minutes, whereas each noun/verb block included 96 trials and lasted approximately 4 minutes. In total, there were 448 trials per subject in the sentence condition and 384 trials in each single word condition (therefore 768 trials in total in the single word condition). In both sentence and single word conditions, each block included 50% masked and 50% unmasked trials, randomly mixed within blocks.

In masked trials, we presented a fixation cross (300 ms), a blank screen (200 ms), a first mask (67 ms), a first prime (33 ms), a second mask (67 ms), a second prime (33 ms), a third mask (67 ms), a third prime (33 ms), a fourth mask (67 ms) and a target picture (1000 ms). After the picture, a fixation cross appeared on the screen until an answer was given (see **Figure 2.1A** and **2.1C** for examples of the trial structure). After the answer, the fixation cross turned green and a new trial started. In unmasked trials, we presented a fixation cross (300 ms), a blank screen (200 ms), a first blank (67 ms), a first prime (67 ms), a second blank (33 ms), a second prime (67 ms), a third blank (33 ms), a third prime (67 ms), a fourth blank (33 ms) and a target picture (1000 ms), followed by a fixation cross. Unmasked primes had a longer duration than the masked primes in order to increase the visibility of the middle word, which otherwise would have been partially masked by the first and third words. In order to keep the duration of a trial constant (i.e. 1867 ms) across masking strength conditions, the duration of blanks in the unmasked condition was adjusted accordingly.

Participants were instructed to respond to the target picture only after the fixation cross appeared on screen. They had to indicate whether the picture matched or did not match with the previous sentence/word by pressing either a left or a right key on the keyboard with their left or right hand, respectively. Crucially, in the sentence condition, participants needed to combine the three words into a sentence in order to perform the task correctly.

In order to make the task meaningful in the masked condition, participants were told that each block included “easy” and “difficult” trials. In the difficult trials, words were “hidden”, which made them very hard to be read. However, they had to try their best to respond correctly. Therefore, participants were aware that words were present in the masked condition, but they were not able to perceive them clearly. There was no speed stress on the response. Each block included 50% congruent and 50% incongruent trials, randomly mixed within blocks. The interval between trials varied between 750 and 1250 ms, drawn from a random distribution. From now on, we will refer to these word-picture trials as "picture trials".

In order to assess prime visibility, participants performed a forced-choice discrimination task in approximately 15% of the masked trials (i.e. 16 for the sentence blocks and 12 for the noun/verb blocks). Here, instead of a picture, a four-option screen occurred after masked primes. Participants were asked to decide which sentence or word they had just seen, and pick the correct option among the four presented. The four choices were presented in lowercase letters and around fixation, in a squarewise configuration. The correct choice was presented equally across the four possible positions around fixation (up-left, up-right, low-left, low-right). In the sentence condition, incorrect choices were equally divided across three incongruency subcases, as in the picture trials (incongruent actors/congruent action; congruent actors/incongruent action; incongruent actors/incongruent action). From now on, we will refer to these trials as “discrimination trials”. Note that, in the main task, participants also needed to discriminate words in order to perform the match/no match task correctly. Therefore, the main task could also be employed to evaluate prime visibility. The forced-choice discrimination task was added as a more traditional and supplementary visibility check. At the end of each block, performance feedback was provided on participants’ accuracy, for both masked and unmasked trials.

2.2.4. Procedure

The experiment consisted of two separate sessions on separate days. In the first session, participants performed a short version of the task for 6 blocks (2 sentence, 2 noun and 2 verb blocks), with no EEG recording, in order to familiarize themselves with the task. They were introduced to both task and stimuli before starting the measurement. During the second session (1-7 days after the first), participants performed the main task (12 blocks: 4 sentence, 4 nouns and 4 verb blocks) and EEG was recorded. Before starting the EEG recording, participants were briefly reminded both task and stimuli and performed one practice block, randomly selected across block types. In both sessions, block order was randomized across participants.

2.2.5. Electroencephalographic measurements

The electroencephalogram was recorded continuously from 61 active Ag/AgCL electrodes using an actiCap system (Brain Products GmbH). 59 of these electrodes were mounted on a cap with equidistant electrode montage. Two separate electrodes were placed on the left and right mastoid, respectively. Blinks were monitored through a separate electrode placed below the left eye and the closest frontal electrodes to the left eye. Horizontal eye movements were monitored through two electrodes placed on the lateral canthi next to the left and right eye. The ground electrode was placed on the forehead. EEG and EOG recordings were amplified through BrainAmp DC amplifiers. The EEG signal was recorded with a sampling rate of 500 Hz and filtered offline with a high-pass filter of 0.1 Hz and a low-pass filter of 40 Hz. All electrode sites were re-referenced offline to the average of left and right mastoids and epoched from -0.867 (i.e. the beginning of a trial) to +1 s surrounding each trial. All ERPs were time-locked to target, i.e. picture, presentation. Next, trials were visually inspected and those containing artefacts not related to blinks were manually removed. Note that visual inspection was blind to the conditions of the experiment. Deleted channels were reconstructed based on a nearest neighbor approach. Independent component analysis (ICA) was computed and components containing blink/oculomotor artefacts were removed from the data. The pre-target interval between 567 and 367 ms before target (i.e. the duration of the blank before the first mask) was employed as a baseline.

2.2.6. Statistical analyses

Behavioral analyses (repeated measures ANOVAs and paired t-tests) were performed with in-house MATLAB (The Mathworks, Natick, MA, USA) scripts. For our ERP analyses, all preprocessing steps were conducted with Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). ERP statistical analyses were performed using a combination of Fieldtrip and in-house MATLAB scripts. We focused on the N400 effect, defined as a difference in amplitude between two N400 components, i.e. negative event-related potentials (ERPs) evoked by meaningful stimuli (Baggio & Hagoort, 2011). Since its discovery, the N400 effect has been consistently observed in response to semantic violations (Kutas & Hillyard, 1980), although it is also known to be evoked by violations of context, expectancies and world knowledge (Baggio & Hagoort, 2011; Kutas & Federmeier, 2010; Lau, Phillips, & Poeppel, 2008). Previous studies showed that N400 usually peaks at centroparietal electrodes, although sometimes more anteriorly (Kutas & Federmeier, 2010; Lau et al., 2008). The typical N400 time window is 250-550 ms, although this may vary as well (Kutas & Federmeier, 2010; Lau et al., 2008). Thus, our strongest hypothesis was formulated around the polarity of the N400 effect, in that we expected a negative difference between incongruent and congruent trials.

As a first step, we performed cluster-based permutation tests (Maris & Oostenveld, 2007) on the time window 0-1 s from target (i.e. picture) onset to isolate significant ERP effects related to semantic incongruency (contrast incongruent vs. congruent, all conditions collapsed). A minimum of two neighboring electrodes had to pass the threshold of $p<0.05$ to form a cluster. Cluster-based procedure was repeated 10000 times. This Monte-Carlo method generated a nonparametric estimate of the p-value representing the statistical significance of the originally identified cluster. This analysis isolated significant effects as clusters in time and space (in our case, the N400 effect). To visualize the evolution of significant clusters, we divided the time period (0-1 s) in 10 equal bins and plotted for each bin (i.e. 0-100, 100-200, etc.) all electrodes that were significant at least 50% of the time (as an example, cf. **Figure 2.2A**). Subsequently, for follow-up analyses we isolated the exact time window and channels where the N400 effect was significant. To do so, the onset and offset of a cluster were defined as the time period around the maximum difference where the difference did not drop below 50% of this maximum and where at least one channel showed a significant effect. We then selected the 10 channels within the cluster that showed the largest effect in this time window (for a similar procedure, cf. Meijs et al., 2018). The resulting region of interest (ROI) and time window were used for subsequent analyses including all the relevant factors. Note that, as a “sanity check”, all analyses were also performed on a central ROI, defined based on previous literature on the N400 (Kutas & Federmeier, 2010). These supplementary analyses led to the same conclusions.

2.3. Results

Our goal was to investigate whether semantic unification requires neural feedback between distant brain areas. We addressed this issue by interfering with feedback processing by means of visual masking, and comparing masked and unmasked processing of sentences and single words.

2.3.1. Behavior

2.3.1.1. Day 1 (behavioral training)

In these analyses, 36 out of the 40 participants were included, because the first four participants passed a slightly different version of the task in the training session. Overall, we observed that masking strength affected participants' accuracy (main effect of masking strength: $F_{1,35}>1000$, $p<0.001$), and that this effect was modulated by the semantic complexity of the primes (sentences vs. single words) (interaction masking strength x semantic complexity: $F_{1,35}=4.24$, $p=0.047$). Follow-up analyses revealed that performance was higher in the unmasked than in the masked condition (sentences: $t_{35}=23.35$, $p<0.001$; single words: $t_{35}=45.37$, $p<0.001$). In the unmasked condition, performances were very high and strongly above chance (sentences: $t_{35}=31.70$, $p<0.001$, 90% correct; single words: $t_{35}=120.43$, $p<0.001$, 98% correct). Although performance was poor in the masked condition, it was also above chance level (sentences: $t_{35}=3.66$, $p<0.001$, 54% correct; single words: $t_{35}=10.21$, $p<0.001$, 58% correct).

In forced-choice discrimination trials, masked words were also poorly discriminated (sentences: 29% correct; single words: 35% correct), although subjects scored significantly above chance level (sentences: $t_{35}=3.12$, $p=0.003$; single words: $t_{35}=6.9$, $p<0.001$). Note that chance level was 25% in this case, given that the task required a choice among four response options.

2.3.1.2. Day 2 (EEG recording)

Participants performed similarly on day 1 and day 2 on the main task (all p-values>0.063). Further, as on day 1, we observed that masking strength affected participants' accuracy (main effect of masking strength: $F_{1,39}>1000$, $p<0.001$) and performance was modulated by semantic complexity (interaction masking strength x semantic complexity: $F_{1,39}=10.1$, $p=0.003$). Again, performance was higher in the unmasked than in the masked condition (sentences: $t_{39}=37.77$, $p<0.001$; single words: $t_{39}=54.31$, $p<0.001$. **Figure 2.1B** and **2.1D**). In the unmasked condition, subjects scored very high and strongly above chance (sentences: $t_{35}=38.44$, $p<0.001$, 92% correct; single words: $t_{35}=195.33$, $p<0.001$, 98% correct. **Figure 2.1B** and **2.1D**). Although performance was poor in the masked condition, it was above chance level (sentences: $t_{39}=5.63$, $p<0.001$, 54% correct; single words: $t_{39}=9.06$, $p<0.001$, 57% correct. **Figure 2.1B** and **2.1D**). Moreover, we found that in single word trials, prime position affected participants' accuracy (main effect of prime position: $F_{2,78}=6.25$, $p=0.003$) and was modulated by masking strength (interaction prime position x masking strength: $F_{2,78}=5.42$, $p=0.006$). In the unmasked condition performance was equal in all prime positions (~98%

correct in all positions, $F_{2,78}$=0.22, p=0.790), whereas in the masked condition it was lower when the prime was presented later in the trial (prime position 1: 60% correct, prime position 2: 56% correct, prime position 3: 54% correct, $F_{2,78}$=5.93, p=0.004), despite being above chance in all cases (all p's<0.001).

In forced-choice discrimination trials, there was no significant difference between day 1 and day 2 (p=0.853). As in the main task, masked words were poorly perceived (sentences: 29% correct; single words: 34% correct), although again subjects scored significantly above-chance level (sentences: t_{39}=4.63, p<0.001; single words: t_{39}=6.59, p<0.001).

Overall, the behavioral results revealed that participants perceived masked and unmasked trials very differently, as revealed by the fact that accuracy was much lower in the masked than in the unmasked condition (although accuracy was above chance in the main task as well as in the discrimination task for masked trials). This suggested that participants may have been partially aware of masked primes, most likely due to the nature of the task (they were told that in some trials words were present, but very difficult to be seen – see the Methods section for further details). Therefore, masking led to a quantitative difference in visibility ("matter of degree") rather than a qualitative difference.

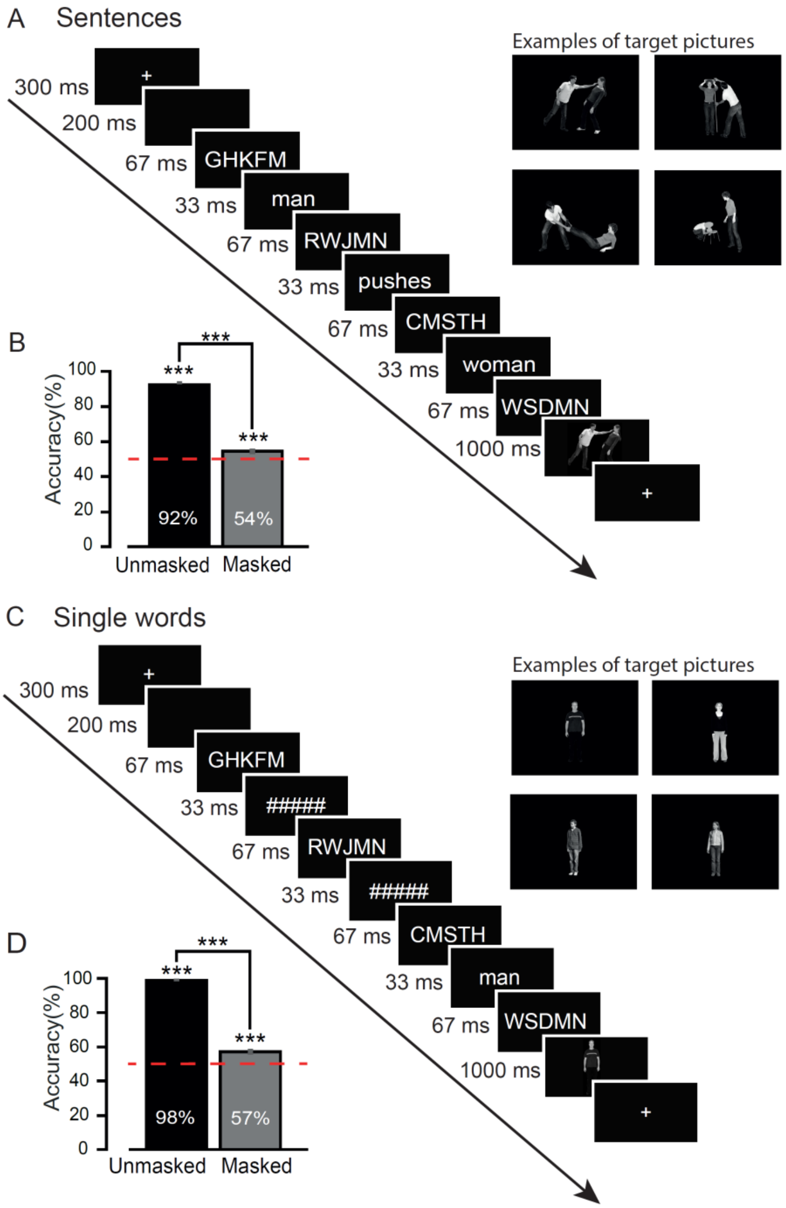

Figure 2.1: Paradigm and behavioral results. (A) Left panel: trial structure in the masked sentence condition. Three masked words forming a sentence were sequentially presented and followed by a target picture, which could be congruent or incongruent with the previous sentence. In the figure, a congruent trial is represented. When the fixation cross appeared after the picture, participants performed a match/no match task. Right panel: example of target pictures employed

in the sentence condition. **(B)** Participants' accuracy in the sentence condition, for unmasked (black) and masked (grey) trials separately. Results are presented for Day 2 only. Error bars represent between-subject SEM. **(C)** Left panel: trial structure in the masked single word condition. One word occurring in the first, second or third prime position was presented and followed by a picture, either congruent or incongruent with the previous word. In the figure a congruent, third-position trial is represented. Right panel: example of target pictures employed in the single word condition. **(D)** Participants' accuracy in the single word condition, for unmasked (black) and masked (grey) trials separately. Results are presented for Day 2 only. Error bars represent between-subject SEM.

2.3.2. ERP analyses

Next, we investigated whether neural signatures of semantic processing, reflected in the N400 effect, could be found for masked/unmasked sentences and single words. To this end, we contrasted congruent and incongruent trials using cluster-based permutation testing, correcting for multiple comparisons across both time (0-1 s) and (electrode) space (see **Figure 2.2A** and Methods, Maris & Oostenveld, 2007). When isolating significant effects as clusters in time and space (see Methods), we found a significant difference over centro-parietal electrodes from 336-598 ms after target onset and peaking at 490 ms (see **Figure 2.2A**), consistently with a typical N400 time window and topography (p-value of the cluster between 336-598 ms: $p<0.001$).

Within this cluster, we performed repeated measures ANOVAs on the N400 time window with three factors: masking strength (masked/unmasked), prime/target congruency (congruent/incongruent), and semantic complexity (sentence/single word) to test how, and if, the N400 effect was modulated by masking strength and semantic complexity. This ANOVA revealed that the N400 effect (main effect of congruency: $F_{1,39}=104.06$, $p<0.001$) was larger for unmasked than masked trials (interaction masking strength x congruency: $F_{1,39}=66.80$, $p<0.001$). Additionally, we found that the overall ERP amplitude was larger for unmasked than masked trials (main effect of masking strength: $F_{1,39}=13.76$, $p<0.001$). No other main effects or interactions were significant (all p-values>0.234). Overall, these results show that the N400 effect was modulated by prime visibility. Therefore, in further planned post-hoc analyses we tested the N400 effect for masked and unmasked trials separately.

In the unmasked condition, a clear N400 effect was observed (main effect of congruency: $F_{1,39}=94.42$, $p<0.001$), which was not modulated by semantic complexity (interaction of congruency x semantic complexity: $F_{1,39}=1.77$, $p=0.190$). In both unmasked semantic complexity conditions, an N400 effect was observed (sentences: t_{39}=6.73, p<0.001; single words: t_{39}=9.49, p<0.001, **see Figure 2.2B**).

In contrast, in the masked condition we did not find a significant N400 effect regardless of semantic complexity (main effect of congruency: $F_{1,39}$=2.21, p=0.145; interaction of congruency x semantic complexity: $F_{1,39}$=0.002, p=0.961). Given our hypotheses, we tested the congruency effect for sentences and single words separately, but no N400 effect was present in either condition (sentences: $t_{39=}$0.78, p=0.439; single words: t_{39}=1.21, p=0.232).

Still, in our paradigm, single words could occur in different prime positions. Previous studies have shown that the SOA between prime and target affects the strength of semantic priming (Greenwald et al., 1996; Kiefer, 2002; Kiefer & Brendel, 2006; Nakamura et al., 2018). Therefore, we investigated whether prime position affected N400 amplitude. To do so, we split the trials according to the prime position, i.e. first, second and third, and used this as additional factor in an ANOVA. We found that prime position affected the N400 effect for single words in the masked condition (interaction congruency x position: $F_{2,78}$=3.40, p=0.038), but not in the unmasked condition (interaction congruency x position: $F_{2,78}$=0.51, p=0.603). Interestingly, post-hoc t-tests revealed that an N400 effect for masked single words was only present when the prime was presented in the third position, i.e. immediately before target presentation (t_{39}=2.48, p=0.017, see **Figure 2.2C**). In the other prime positions no significant N400 effect was observed (second prime position: t_{39}=1.10, p=0.274; first prime position: t_{39}=1.13, p=0.261).

In summary, our results for the unmasked condition revealed an N400 effect for both sentences and single words, whereas in the masked condition we only found an N400 effect for single words occurring in the third prime position, i.e. just before picture presentation.

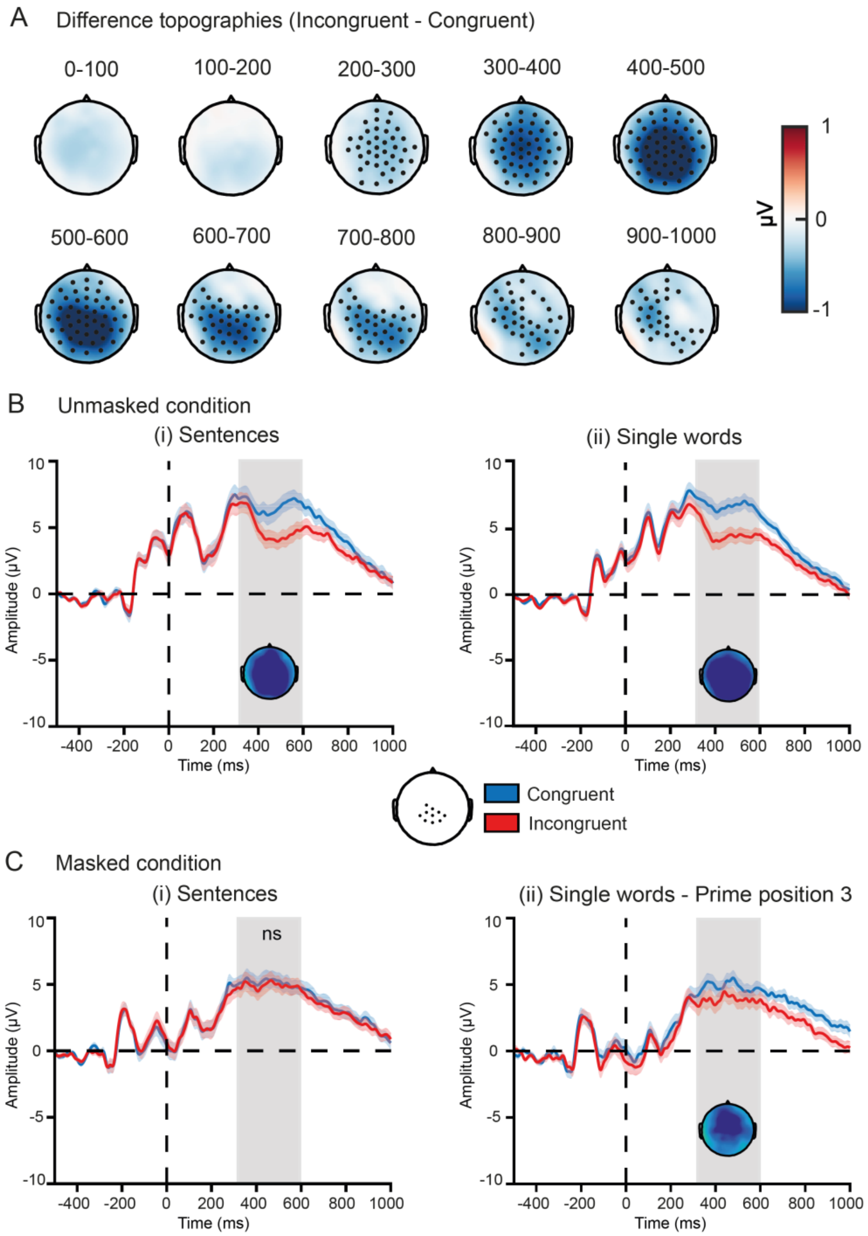

Figure 2.2: N400 ERP effect. (A) Topographic maps of the difference between incongruent and congruent trials over time (0 = target, i.e. picture onset). Cluster-based permutation tests were used to isolate the significant effects, while correcting for multiple comparisons across time and (electrode) space. On each head map, channels with a significant effect for at least 50% of its time window are

highlighted. **(B)** ERPs for a central region of interest (see inset) for congruent (blue) and incongruent (red) unmasked trials, in the sentence (i) and single word (ii) condition. **(C)** ERPs for congruent (blue) and incongruent (red) masked trials, for sentences (i) and single words occurring in the third prime position (ii). Inset represents the channels within the cluster that showed the largest effect in the time window 336-598 ms. In all figures shaded blue and red areas around the wave form indicate between-subject SEM. Time 0 represents the onset of the target picture. Shaded grey areas highlight the time window of interest for the N400 effect (336-598 ms). All headmaps are scaled from -1 to 1 microvolts.

2.4. Discussion

In this study, we investigated the neural mechanisms underpinning sentence and single word processing, focusing on the difference between semantic unification and lexical retrieval processes under varying levels of awareness. According to the Memory, Unification and Control (MUC) model, feedback from the left inferior frontal cortex (LIFC) to the left posterior temporal cortex (LPTC) is crucial for semantic unification, i.e. the process in which words meanings are flexibly combined into a sentence (Hagoort, 2005, 2013, 2017). On the contrary, lexical retrieval (i.e. single word processing) is thought to rely on a feedforward information flow from sensory regions to the LPTC. Here we tested the general claim that long-range feedback is required for semantic unification, but not for lexical retrieval. To this aim, we reduced stimulus awareness with visual masking, which is thought to disrupt long-range connectivity within the brain (Del Cul, Baillet, & Dehaene, 2007; Del Cul et al., 2009). We investigated whether, when disrupting long-range feedback with masking, semantic unification could still occur. To do so, we designed a novel experimental paradigm in which we directly compared semantic unification and lexical retrieval mechanisms.

Using EEG, we measured brain responses to sequentially presented words forming a sentence and single words in a masked priming task. Three masked/unmasked words composing a short sentence (e.g. *man-pushes-woman*) were followed by a picture, either congruent or incongruent with the previous sentence. This sentence condition was compared with a single word condition, in which either a noun (e.g. *man*) or a verb (e.g. *pushes*) was followed by congruent/incongruent pictures. Importantly, single words occurred in the first, second or third prime position, i.e. at different stimulus onset asynchronies (SOAs).

Behaviorally, performance on the word(s)-picture matching task was higher in the unmasked than in the masked condition. Therefore, masking strongly reduced prime visibility. In EEG, in the unmasked condition we found an N400 effect for both unmasked sentences and single words. On the contrary, in the masked condition we did not observe any N400 effect for sentences. In the single word condition, we only found an N400 effect for single words occurring in the third prime position (i.e. just before picture presentation), which supports the claim that masked word processing is dependent on the SOA between prime and target (Greenwald et al., 1996; Kiefer, 2002; Kiefer & Brendel, 2006; Nakamura et al., 2018) and that, more generally, masked visual information is fleeting. It is unlikely that this effect was driven by prime visibility, because our behavioral results showed that performance (visibility) for third-position primes was actually lower than in the other two prime positions.

The absence of the N400 effect for masked sentences may mean that semantic unification cannot be performed when disrupting feedback processing with masking. However, in this experimental paradigm, sentences were presented sequentially, i.e. word by word. Given that, in the single word condition, we only found an effect for words presented at a short SOA, this null result could stem from the sequential presentation of the primes. If in the sentence condition the information conveyed by the first two words decayed very quickly, combining the three words into a sentence would not be possible.

Moreover, a recent study by van Gaal et al. (2014) found that two masked words (negation+ adjective, e.g. *not good*) can be integrated under reduced awareness, although only after subjects were extensively trained on the task (van Gaal et al., 2014). The paradigm employed by van Gaal et al. is comparable to our paradigm, in terms of both masking technique and timing of stimulus presentation, although the target was a picture in our study and a word in van Gaal et al.'s study. One may thus argue that, in contrast to this study, they found an effect because two-word integration is easier than three-word integration, which may be too effortful under reduced awareness. Indeed, processing under reduced awareness is very limited compared to fully conscious processing, both in terms of attentional allocation and working memory load (Dehaene et al., 2006; Lamme, 2006).

Finally, in this study we employed target pictures with one character in the noun trials, whereas in the sentences and verb trials we employed pictures with two characters. Therefore, it may be that prime-target match in the noun case was easier compared to the other two cases. This could lead to task-related differences between the noun and sentence/verb conditions.

To overcome these limitations, we performed an additional experiment in which two words (instead of three) were presented simultaneously and at a short SOA. In order to minimize task-related differences, we employed the same two-character pictures in all conditions. We reasoned that, if we replicated our previous findings, this would suggest a true difference between sentence and single word processing, not biased by task-related effects or by the fleeting nature of masked word processing. Issues related to both this study and its follow-up will be jointly discussed in the Discussion section of the following chapter.

3

Is feedback processing necessary for semantic unification? How awareness affects simultaneously presented sentences

This chapter appeared in: Mongelli, V., Meijs, E. L., van Gaal, S., & Hagoort, P. (2019). No language unification without neural feedback: How awareness affects sentence processing. *NeuroImage*, *202*, 1–12. (Experiment 2)

Abstract

According to the Memory, Unification and Control (MUC) framework, semantic unification is realized in a dynamic interplay between the left inferior frontal cortex (LIFC) and the left posterior temporal cortex (LPTC), whereas lexical retrieval (single word processing) relies on feedforward mechanisms within the LPTC. In previous work, we tested the claim that feedback processing is required for semantic unification but not for lexical retrieval. To do so, we disrupted feedback processing through visual masking, which impairs long-range feedback processing while preserving feedforward processing. In an electroencephalography (EEG) experiment, subjects performed a priming task in which masked/unmasked sentences or single words were judged as congruent or incongruent with respect to a target picture. Importantly, single words occurred at different stimulus onset asynchronies (SOAs). We focused on the N400 effect as a typical neural signature of semantic incongruency. Our findings showed an N400 effect for both sentences and single words in the unmasked condition, and only for single words occurring at the shortest SOA in the masked condition. Since in the sentence condition words were presented sequentially, the absence of an effect could be due to the fleeting nature of masked visual processing. To overcome this limitation, we performed a follow-up EEG experiment in which 40 subjects performed a similar masked priming task, in which words in the sentence condition were simultaneously presented. We found an N400 effect for masked single words and not for sentences, replicating our previous findings. Overall, our results suggest that long-range feedback processing is required for semantic unification, but not for lexical retrieval.

3.1. Introduction

Language comprehension is more than retrieving single word meanings from memory and concatenating them. It also requires putting these meanings into context and unifying them in order to form a novel meaning at the sentence level. Combinatorial processing, here defined as unification (Hagoort, 2005, 2013, 2017), is a landmark of language processing across all representational domains (Jackendoff, 2002). According to the Memory, Unification and Control (MUC) model, semantic unification is performed in a dynamic interplay between the left inferior frontal cortex (LIFC) and the left posterior temporal cortex (LPTC), whereas lexical retrieval (single word processing) relies on feedforward processing within the LPTC (Hagoort, 2017; Hultén et al., 2019).

In previous work, reported in Chapter 2, we tested the claim that long-range feedback processing, likely involving frontal and temporal areas, is required for semantic unification, but not for lexical retrieval. We employed visual masking to disrupt feedback and investigated whether, under these conditions, semantic unification processes were spared. Masking is thought to impair feedback between distant brain areas, while preserving feedforward processing (Del Cul et al., 2009; Fahrenfort et al., 2007, 2017; Lamme & Roelfsema, 2000). In an electroencephalography (EEG) masked priming experiment, we compared sentence and single word processing focusing on the N400 effect, a typical signature of semantic incongruency (Kutas & Federmeier, 2010; Kutas & Hillyard, 1980). It has been shown that, at least under certain conditions, masked single words still trigger an N400 effect (Kouider & Dehaene, 2007), while the possibility of masked combinatorial processing is more controversial (Rabagliati et al., 2018; Rohaut & Naccache, 2018). In the sentence condition, masked/unmasked words forming a short sentence (e.g. *man-pushes-woman*) were presented sequentially (i.e. word by word) and followed by a target picture, which could be either congruent or incongruent with the previous sentence. In the single word condition, masked/unmasked words (nouns and verbs) appearing at different stimulus onset asynchronies (SOAs)[9] were also followed by congruent/incongruent pictures.

Our results showed that both unmasked sentences and single words triggered a robust N400 effect. On the contrary, in the masked condition an N400 effect was only found for masked single words occurring at the shortest SOA, i.e. just before picture presentation. The absence of an effect in the masked sentence condition may suggest that masking impairs semantic unification, which may therefore rely on feedback processing. However, since in our paradigm words composing the sentence were sequentially presented, this null result may also be caused by the

---

[9] SOA is the time from mask onset to target onset.

fleeting nature of masked visual processing. Indeed, previous studies have shown that masked semantic priming is more likely to occur at short SOAs (Greenwald et al., 1996; Kiefer, 2002; Kiefer & Brendel, 2006; Nakamura et al., 2018).

A second limitation of the previous experiment is that we employed different target pictures in the noun and sentence/verb conditions. This may have introduced task-driven effects in our results. Finally, in a study with very similar experimental settings, van Gaal et al. (2014) found that two masked words (negation+adjective, e.g. *not good*) may trigger an N400 effect (van Gaal et al., 2014). Since processing capacities under reduced levels of awareness are very limited (Dehaene et al., 2006; Lamme, 2006), it may be that they found an effect simply because they employed two words, whereas we employed three words in the sentence condition. In this case, the null result of the previous study would not be caused by specific differences between semantic unification and lexical retrieval. Employing two-word sentences instead of three-word sentences would rule out this alternative explanation.

To overcome these limitations, we ran a follow-up experiment in similar experimental settings. The main differences were in the sentence condition, in which we simultaneously presented two-word combinations at a short SOA. Moreover, we aimed to minimize task-related differences by employing the same target pictures across all conditions. We reasoned that, if we replicated our previous findings, the null result in the sentence condition would confirm that feedback disruption selectively impairs semantic unification processes.

3.2. Material and Methods

3.2.1. Participants

40 subjects (25 females) participated in this study. All subjects were right-handed native Dutch speakers, aged between 18 and 35, had normal or corrected-to-normal vision, no neurological history and were naive to the purpose of the experiment. Subjects gave written informed consent prior to participation, according to the Declaration of Helsinki. They received 56 euros for their participation.

3.2.2. Stimuli

In the sentence condition, we employed two-word combinations composed by either agent/action pairs (e.g. *man pushes*, in Dutch *man duwt*) or patient/action pairs (e.g. *man is pushed*, in Dutch *man geduwd*). We will refer to these combinations as sentences. As in the previous experiment, sentences were obtained by combining words that are not lexically related with each other. Contrary to the previous experiment, the two words forming the sentences were presented one above the other. In the noun and verb conditions, we employed respectively the same four nouns and four active/passive verbs that were used in the sentence condition. The nouns employed to fill the agent/patient roles were the following: *man, woman, boy, girl* (in Dutch: *man, vrouw, jongen, meisje*). The verbs employed to fill the action role were the following: (i) active verbs: *pushes, measures, drags, finds* (in Dutch: *duwt, meet, sleept, vindt*); (ii) passive verbs: *is pushed, is measured, is dragged, is found* (in Dutch: *geduwd*, *gemeten*, *gesleept*, *gevonden*). Nouns and active verbs were the same as in the previous experiment.

As in the previous experiment, sentences and single words were followed by a picture, either congruent or incongruent with the previous sentence/word (**Figure 3.1A**). We employed the same, previously tested picture database (Menenti et al., 2011). Pictures portrayed transitive events like *pushing* or *dragging*, together with the agent and patient of the event. Within each picture there were two actors (one male and one female, either both children or both adults). One of the two actors (the male or the female) played the agent role. The agent position (right or left) was randomized. Menenti et al. (2011) tested the database to verify whether the events described were informative enough. Next, they selected the verb that was most frequently used to describe each action in order to form the verb-picture pair.

Pictures had a size of 400x300 pixels. Masks were created in the same way as in the previous experiment, i.e. randomly presenting strings of uppercase letters, which were slightly overlapping in order to augment mask density. However, since in the case of passive verbs masked words were slightly longer than active verbs, we increased the number of letters composing each mask (ten letters instead of seven). As in the previous experiment, the space between the center of each letter was 10 pixels. Both words and masks were presented in Arial lowercase font with a size of 20. Word(s) stimuli were presented in white against a black background. Participants' distance from the monitor was approximately 110 cm.

3.2.3. Experimental design

The experiment was programmed using Presentation software (Neurobehavioral Systems, Albany, NY, USA). As in the previous experiment, we employed a 2 (primes semantic complexity: sentence or single word) x 2 (target congruency: congruent or incongruent) x 2 (masking strength: masked or unmasked) factorial design. In the sentence condition, we built incongruency by reversing the actors' roles in the picture (e.g. if the prime was *man pushes*, then the picture depicted a woman pushing a man; if the prime was *man is pushed*, then the picture depicted a man pushing a woman). In both sentence and single word blocks, each block included 96 trials and lasted approximately 5 minutes. Each block included 50% masked and 50% unmasked trials, randomly mixed within blocks.

In masked trials, stimuli presentation was the following: a fixation cross (300 ms), a blank screen (200 ms), a first mask (67 ms), a prime (33 ms), a second mask (67 ms), a target picture (1000 ms) and a fixation cross (200 ms). After the fixation cross, an answer screen with the options *match/no match* (in Dutch: *wel match/geen match*) appeared (see **Figure 3.1A** and **3.1C** for examples of the trial structure). The position of the match answer (left or right) was randomized. In unmasked trials, we presented a fixation cross (300 ms), a blank screen (200 ms), a first blank (67 ms), a prime (67 ms), a second blank (33 ms), a target picture (1000 ms) and a fixation cross (200 ms). The unmasked prime had a longer duration than the masked prime in order to increase its visibility. To keep the duration of a trial constant (i.e. 1867 ms) across visibility conditions, the duration of blanks in the unmasked condition was adjusted accordingly. Due to a programming error, in the noun/verb main EEG session the duration of the second mask in the masked trials was 33 ms, whereas the duration of the second blank in the unmasked trials was 67 ms. However, this did not influence our results, as performances did not differ between the training session and the main EEG session (see the Results section for further details).

Contrary to the experiment reported in Chapter 2, in which pictures in the noun condition only included one character, we employed the same two-character pictures as in the sentence and verb condition, in order to minimize task differences between the sentence and the single word condition. Since the noun primes referred to a single person (*man, woman, boy* or *girl*), and pictures depicted either a man and a woman or a boy and a girl, we employed a color-coded version of the pictures, instead of the greyscale version previously used. The agent was depicted in green and the patient was depicted in red. In the noun condition, participants had to indicate if the green character matched with the prime by pressing a key on the keyboard with their left or right hand (depending on the location of the match/no match answer). In the sentence and verb conditions, participants had to indicate whether the picture matched or did not match the previous sentence/verb. They were instructed to respond to the target picture only after the answer screen appeared. As in the previous experiment, in the sentence condition participants needed to combine the two words into a sentence in order to perform the task correctly.

As in the previous experiment, participants were told that each block included “easy” and “difficult” trials (the unmasked and masked trials, respectively). Although in the difficult trials words were difficult to read, they had to try to answer correctly anyway. There was no speed stress on the discrimination response. In each block there were 50% congruent and 50% incongruent trials, which were randomly mixed within blocks. The between-trial interval was 750-1250 ms, drawn from a random distribution. We will name these trials "picture trials".

Prime visibility was assessed with a forced-choice discrimination task (16 masked trials out of 48 for each block), as in the previous experiment. We will name these trials “discrimination trials”. In this case, masked primes were followed by a four-option screen instead of a picture. Participants were required to select among four options the word(s) they had just seen. The four options were presented in lowercase letters and around a fixation cross, in a square configuration. The correct option occurred in equal percentage across the four possible positions around the fixation cross (up-left, up-right, low-left, low-right). As in the previous study, this forced-choice discrimination task was added as a supplementary visibility check, given that in the main task participants also had to discriminate the prime(s) in order to respond correctly. After every block, participants received feedback on their performance, for masked and unmasked trials together.

3.2.4. Procedure

In this experiment, we increased the number of trials per condition compared to the experiment reported in Chapter 2. A single EEG session would have been too long, hence we split the EEG recording in two sessions. Therefore, in total the experiment consisted of three separate sessions on separate days. In the first session, participants performed a short version of the task for 6 blocks (2 sentence, 2 noun and 2 verb blocks), with no EEG recording, in order to familiarize themselves with the task. They were introduced to both task and stimuli before starting the measurement. During the second session, participants performed 12 sentence blocks while EEG was recorded. During the third session, participants performed 6 noun blocks and 6 verb blocks while EEG was recorded. The second and third sessions were both completed within 1-7 days after the first and their order was counterbalanced across subjects. In the EEG recording sessions, there were 1152 trials in the sentence condition and 576 trials in each single word condition (therefore 1152 trials in total). Before starting the EEG recordings, participants were briefly reminded of task and stimuli and performed one practice block (in the noun/verb session, this was randomly selected across block types). In all sessions, block order was randomized across participants.

3.2.5. Electroencephalographic measurements

Electroencephalographic measurements and parameters, which were the same as in the previous experiment, are reported below. The electroencephalogram was recorded continuously from 61 active Ag/AgCL electrodes with an actiCap system (Brain Products GmbH). 59 of these electrodes were mounted on a cap with equidistant electrode montage. Two separate electrodes were placed on the left and right mastoid, respectively. Blinks were monitored through a separate electrode placed below the left eye and the closest frontal electrodes to the left eye. Horizontal eye movements were monitored through two electrodes placed on the lateral canthi next to the left and right eye. The ground electrode was placed on the forehead. EEG and EOG recordings were amplified through BrainAmp DC amplifiers. The EEG signal was recorded with a sampling rate of 500 Hz and filtered offline with a high-pass filter of 0.1 Hz and a low-pass filter of 40 Hz. Electrode sites were re-referenced offline to the average of left and right mastoids. The only difference with respect to the previous experiment was data epoching, which in this case was performed from -2 to 2.5 s surrounding each trial. All event-related potentials (ERPs) were time-locked to target (picture) presentation. Visual inspection was then performed on trials, and trials containing artifacts not related to blinks were removed manually. Note that visual inspection was blind with respect to experimental conditions. Channel reconstruction was performed based on the nearest neighbor approach. Next, we computed independent component analysis (ICA) and removed components containing blink/oculomotor artefacts. We performed a baseline correction with the pre-target interval between 367 and 167 ms before target (i.e. the duration of the blank before the first mask).

3.2.6. Statistical analyses

We performed behavioral analyses (repeated measures ANOVAs and paired t-tests) in MATLAB (The Mathworks, Natick, MA, USA). For ERP analyses, preprocessing steps were performed in Fieldtrip (Oostenveld et al., 2011). ERP statistical analyses were performed using a combination of Fieldtrip and MATLAB scripts. As in the previous experiment, we focused on the N400 effect as a neural signature of semantic incongruency (Kutas & Hillyard, 1980)[10].

For the ERP analyses, first we performed cluster-based permutation tests (Maris & Oostenveld, 2007) on the time window 0-1 s from target (i.e. picture) onset, in order to isolate significant ERP effects related to semantic incongruency

---

[10] For a more detailed description of N400 timing and topography, see the Methods section of Chapter 2.

(contrast incongruent vs. congruent, all conditions collapsed). A minimum of two neighboring electrodes had to pass the threshold of $p<0.05$ to form a cluster. We repeated the cluster-based procedure 10000 times. This Monte-Carlo method generated a nonparametric estimate of the p-value representing the statistical significance of the originally identified cluster. This analysis isolated significant effects as clusters in time and space (in this case, the N400 effect). In order to see the evolution of significant clusters, we divided the time period (0-1 s) in 10 equal bins and plotted for each bin (i.e. 0-100, 100-200, etc.) all electrodes that were significant at least 50% of the time (as an example, cf. **Figure 3.2A**). Next, we isolated the time window and channels in which the N400 effect was significant. To do so, we defined the onset and offset of a cluster as the time period around the maximum difference in which the difference did not drop below 50% of this maximum, and in which at least one channel showed a significant effect. Subsequently, we selected the 10 channels within the cluster that showed the largest effect within this time window (cf. Meijs et al., 2018 for a similar procedure). The resulting region of interest (ROI) and time window were used for subsequent analyses including all the relevant factors. As in the previous experiment, we also performed all analyses on a central ROI, defined based on previous literature on the N400 (Kutas & Federmeier, 2010), as a “sanity check”. These additional analyses led to the same results.

3.3. Results

In this experiment, we compared EEG responses to simultaneously presented words forming a sentence with responses induced by single words (nouns and verbs). We reasoned that if we replicated findings of the previous experiment, i.e. if we found an N400 effect for masked single words and not for masked sentences, we could conclude that semantic unification cannot be performed under reduced awareness. On the contrary, finding an N400 effect for both masked sentences and single words would mean that the null result in Chapter 2 could be explained by primes sequential presentation in the sentence condition.

3.3.1. Behavior

3.3.1.1. Day 1 (behavioral training)

Overall, we observed that masking strength affected participants’ accuracy (main effect of masking strength: $F_{1,39}>1000$, $p<0.001$), and that this effect was influenced by semantic complexity (sentences vs. single words) (interaction masking strength x semantic complexity: $F_{1,39}= 12.62$, $p=0.001$). In follow-up analyses, we found that performance was higher in the unmasked than the masked condition (sentences: t_{39}=23.04, p<0.001; single words: t_{39}=46.46, p<0.001). For both sentences and single words, performance was poor in the masked condition, although it was at chance level for sentences (t_{39}=1.42, p=0.160, 50% correct) and above chance for single words (t_{39}=5.64, p=<0.001, 53% correct).

In forced-choice discrimination trials, in which chance level was at 25%, masked words were also poorly perceived (sentences: 28% correct; single words: 32% correct), although subjects performed significantly above chance level for both sentences and single words (sentences: t_{39}=2.67, p=0.011; single words: t_{39}=6.97, p<0.001).

3.3.1.2. Day 2 (EEG recording)

Given that the second and third EEG sessions were counterbalanced across subjects, they were both considered as day 2. First, we compared participants' accuracy between the training session and the main session. In unmasked trials, we found a training effect for sentences (t_{39} = 3.62, p<0.001), but not for single words (t_{39}=1.49, p=0.140). In masked trials, as well in the forced-choice discrimination trials, participants performed similarly on day 1 and day 2 (all p-values>0.070). Next, we observed that overall masking strength affected participants' accuracy (main effect of masking strength: $F_{1,39}$>1000, p<0.001), but was not modulated by semantic complexity (interaction masking strength x semantic complexity: $F_{1,39}$=0.06, p=0.80). For both sentences and single words, the masked and unmasked conditions differed significantly, accuracy being significantly lower in the masked condition than in the unmasked condition (sentences: t_{39}=34.64, p<0.001; single words: t_{39}=47.23, p<0.001. **Figure 3.1B** and **3.1D**). In the unmasked condition, subjects scored very high and strongly above chance (sentences: t_{35}=36.46, p<0.001, 90% correct; single words: t_{35}=66.58, p<0.001, 95% correct. **Figure 3.1B** and **3.1D**). Performance was poor in the masked condition for both sentences and single words, but it was at chance level for sentences (t_{39}=0.41, p=0.68, 50% correct) and above chance for single words (t_{39}=7.18, p<0.001, 54% correct. **Figure 3.1B** and **3.1D**).

In forced-choice discrimination trials, masked words were again poorly perceived (sentences: 27% correct; single words: 31% correct), although subjects scored significantly above chance level for both sentences and single words (sentences: t_{39}=2.24, p=0.031; single words: t_{39}=6.07, p<0.001).

In summary, behavioral results in this experiment revealed that performance was significantly worse in the masked than in the unmasked condition. Still, one may ask why in masked sentence trials performance was above chance in the previous experiment (reported in Chapter 2) and at chance in this experiment. This may be explained by the fact that sentence words were presented simultaneously and, as a consequence, participants had less time to perceive and integrate them. Overall, behavioral results in this experiment confirmed our main findings in the previous experiment.

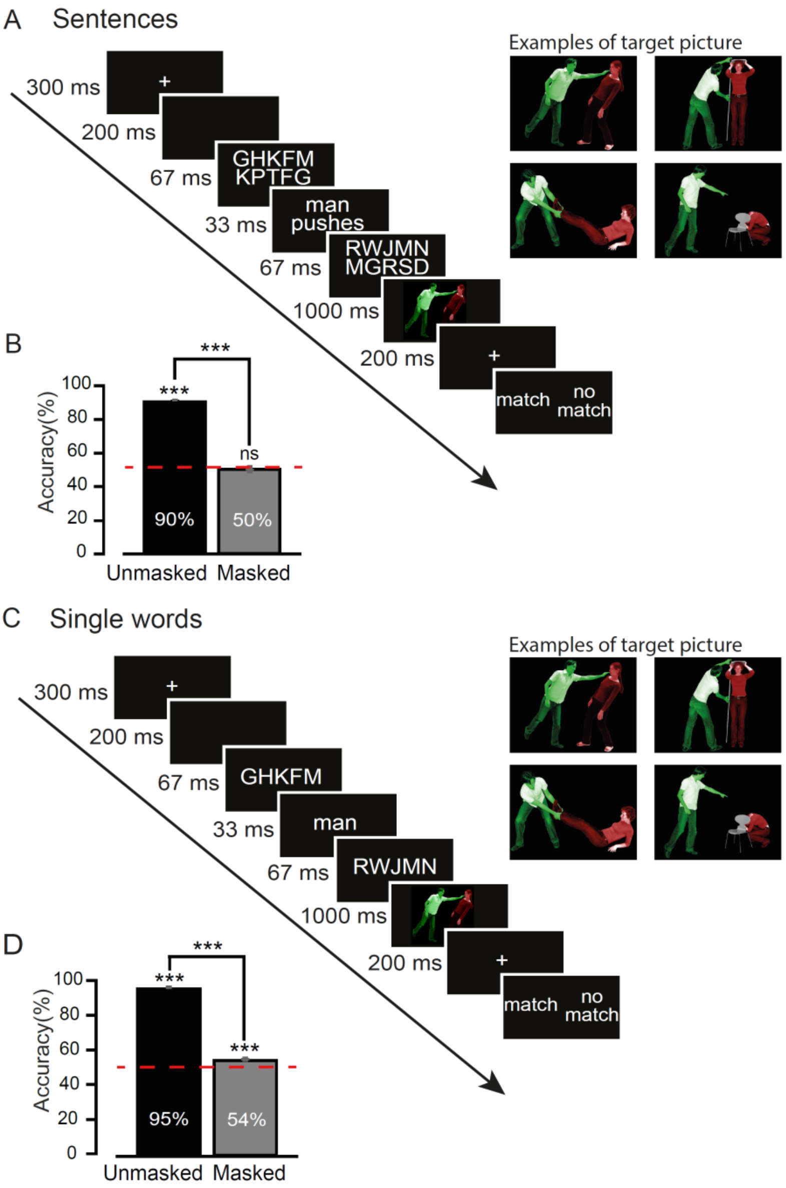

Figure 3.1: Paradigm and behavioral results. (A) Left panel: trial structure in the masked sentence condition. Two masked words forming a sentence were simultaneously presented and followed by a target picture, which could be congruent or incongruent with the previous sentence. In the figure, a congruent trial is represented. Participants performed a match/no match task. Right panel: example of target pictures employed in the sentence condition. **(B)** Participants' accuracy in the sentence condition, for unmasked (black) and masked (grey) trials separately. Results are presented for Day 2 only. Error bars represent between-subject SEM. **(C)** Left panel: trial structure in the masked single word condition. One word was presented and followed by a picture, either congruent or incongruent with the previous word. In the figure a congruent trial is represented. Right panel: example of target pictures employed in the single word condition. Contrary to the previous experiment, target pictures are the same for sentence and single word conditions. **(D)** Participants' accuracy in the single word condition, for unmasked (black) and masked (grey) trials separately. Results are presented for Day 2 only. Error bars represent between-subject SEM.

3.3.2. ERP analyses

Following up on the previous experiment, we investigated whether the N400 effect was modulated for masked/unmasked simultaneously presented sentences and single words. To this end, we performed analyses similarly to the previous experiment. First, we contrasted incongruent and congruent trials employing cluster-based permutation testing, correcting for multiple comparisons across both time (0-1 s) and (electrode) space (see **Figure 3.2A** and Methods section) (Maris & Oostenveld, 2007). When we isolated significant effects as clusters in time and space (see Methods), we found a significant difference over centro-frontal electrodes from 438-708 ms after target onset and peaking at 544 ms (see **Figure 3.2A**; p-value of the cluster between 438-708 ms: $p<0.001$).

Next, we investigated how the N400 effect was modulated by masking strength and semantic complexity. To do so, we performed repeated measures ANOVAs on the N400 time window with three factors: masking strength (masked/unmasked), prime/target congruency (congruent/incongruent) and semantic complexity (sentence/single word). We found that the N400 effect (main effect of congruency: $F_{1,39}=64.76$, $p<0.001$) was larger for unmasked than for masked trials (interaction masking strength x congruency: $F_{1,39}=48.46$, $p<0.001$). This N400 effect was modulated by semantic complexity (interaction congruency x semantic complexity: $F_{1,39}=14.10$, $p<0.001$), as the N400 effect was larger for single words than for sentences. Moreover, there was a marginally significant effect of semantic complexity, suggesting that the overall ERP amplitude may have been slightly higher for sentences than single words (main effect of semantic complexity: $F_{1,39}$=3.69, p=0.062). No other main effects or interactions were significant (all p-values>0.232). Next, in planned post-hoc analyses, we tested the N400 effect for masked and unmasked trials separately, investigating how it was modulated by semantic complexity.

In the unmasked condition, we observed a clear N400 effect (main effect of congruency: $F_{1,39}$=70.48, p<0.001) that was modulated by semantic complexity, being larger for single words than for sentences (interaction of congruency x semantic complexity: $F_{1,39}$=11.45, p=0.001). In both semantic complexity conditions, unmasked incongruent trials triggered a larger N400 effect compared to congruent trials (sentences: t_{39}=4.81, p<0.001; single words: t_{39}=9.46, p<0.001. **Figure 3.2B**).

Although the N400 effect was not significant in the masked condition (main effect of congruency: $F_{1,39}$=0.06, p=0.798), we found that the N400 effect was modulated by semantic complexity (interaction of congruency x semantic complexity: $F_{1,39}$=5.88, p=0.020). This effect was driven by the fact that a significant N400 effect was observed in the single word condition (t_{39}=2.26, p=0.028), but not in the sentence condition (t_{39}=-1.71, p=0.093; if anything the effect was observed in the opposite direction, **Figure 3.2C**).

In summary, in this experiment we replicated the main findings of the previous experiment. In the unmasked condition, we found robust neural signatures of semantic processing, as reflected by N400 effects for both sentences and single words. On the contrary, in the masked condition the N400 effect was only present for single words.

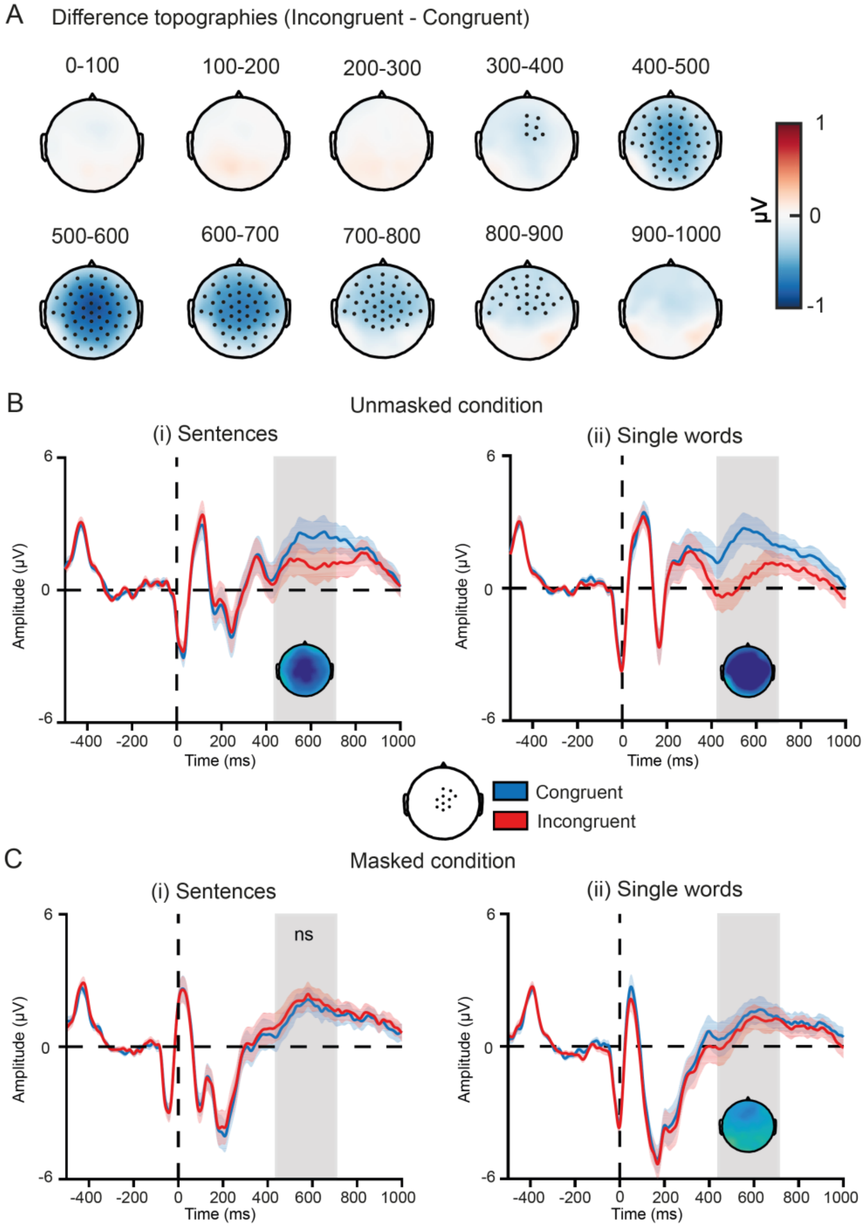

Figure 3.2: N400 ERP effect. (A) Topographic maps of the difference between incongruent and congruent trials over time (0 = target, i.e. picture onset). Cluster-based permutation tests were used to isolate the significant events, while correcting for multiple comparisons across time and (electrode) space. On each head map, channels with a significant effect for at least 50% of its time window are highlighted. **(B)** ERPs for a central region of interest (see inset) for congruent

(blue) and incongruent (red) unmasked trials, in the sentence (i) and single word (ii) condition. **(C)** ERPs for congruent (blue) and incongruent (red) masked trials, for sentences (i) and single words (ii). Inset represents the channels within the cluster that showed the largest effect in the time window 438-708 ms. In all figures shaded blue and red areas around the wave form indicate between-subject SEM. Time 0 represents the onset of the target picture. Shaded grey areas highlight the time window of interest for the N400 effect (438-708 ms). All headmaps are scaled from -1 to 1 microvolts.

3.4. Discussion

In this study, we investigated semantic unification and lexical retrieval under varying levels of awareness. Within the Memory, Unification and Control (MUC) model, feedback from the left inferior frontal cortex (LIFC) to the left posterior temporal cortex (LPTC) is thought to be required for semantic unification, but not for lexical retrieval, which may instead uniquely rely on feedforward processing. To do so, we disrupted long-range feedback with visual masking (Del Cul et al., 2007, 2009; Fahrenfort et al., 2007, 2017; Lamme & Roelfsema, 2000) and investigated whether, under these conditions, semantic unification could still occur.

In previous work, reported in Chapter 2, we measured ERPs in response to sentences and single words in a masked priming task. Three masked/unmasked words forming a short sentence (e.g. *man-pushes-woman*) were sequentially presented and followed by a picture, which was congruent or incongruent with the previous sentence. We compared this sentence condition with a single word condition, with single words occurring at different stimulus onset asynchronies (SOAs). In the unmasked condition, we found a strong N400 effect for both sentences and single words, whereas in the masked condition we only found an N400 effect for single words occurring at the shortest SOA. We reasoned that the absence of an effect in the sentence condition may be due to the fleeting nature of visual processing under reduced awareness (Greenwald et al., 1996; Kiefer, 2002; Kiefer & Brendel, 2006; Nakamura et al., 2018). Moreover, in the previous study we employed different target pictures for noun and sentence/verb stimuli, which could induce task-related differences in the ERP effects. Finally, since a previous study by van Gaal et al. (2014) found ERP effects for two-word masked combinatorial processing (negation+adjective, van Gaal et al., 2014), and given poor and short-living capacities of masked processing (Dehaene et al., 2006), it may be that we did not find any effect because we employed three words (instead of two) in the sentence condition. To clarify these issues, we ran a follow-up experiment in which we compared EEG responses to simultaneously presented two-word sentences and single words, both presented at a short SOA. We minimized task-related differences by employing the same target pictures across all conditions.

Overall, as in the previous experiment, behavioral performance on the word(s)-picture matching task was higher in the unmasked than in the masked condition, suggesting that masking strongly reduced prime visibility. In EEG, incongruent word(s)-picture pairs triggered an N400 effect in both unmasked sentence and single word trials. This is in line with previous work, showing that manipulating semantic congruency within word-picture pairs elicits N400 effects (Coco, Araujo, & Petersson, 2017; Federmeier & Kutas, 2001; Willems, Özyürek, & Hagoort, 2008). On the contrary, in the masked condition, an N400 effect was only observed for single words and not for sentences, confirming previous results.

In summary, we replicated the findings reported in Chapter 2. Taken together, the two experiments suggest that feedback processing may be required for semantic unification, but not for lexical retrieval, which may instead rely on feedforward spreading of activation. We will now discuss issues related to both experiments.

3.4.1. The role of awareness in semantic unification

Our results are consistent with previous work, in which no evidence for semantic unification under reduced awareness was found (Rabagliati et al., 2018; Yang et al., 2017). However, our findings contrast with other work, which suggests that semantic unification under reduced levels of awareness may be possible, to some extent and under certain conditions (Armstrong & Dienes, 2013; Axelrod et al., 2015; Nakamura et al., 2018; Sklar et al., 2012). Nevertheless, these previous findings are either controversial or may be explained by other factors than semantic unification processes.

Axelrod et al. (2015) used continuous flash suppression (CFS) to reduce sentence awareness in functional magnetic resonance imaging (fMRI), and found selective responses in the left frontal cortex to masked sentences compared to unpronounceable nonwords. However, this effect may not be specifically related to semantic unification as sentences and chains of nonwords differ substantially on many low-level semantic aspects, nonwords not involving any word-meaning mapping.

Nakamura et al. (2018) measured the N400 effect triggered by congruent (e.g. *dog-runs*) and incongruent (e.g. *dog-opens*) masked subject/verb pairs within a sentence, while varying the distance between subject and verb across sentences. They found that incongruent pairs triggered an N400 effect only when subject and verb were separated by 0 or 1 word. Although intriguing, these results may reflect simple differences in lexical associations between congruent (*dog-runs*) and incongruent (*dog-opens*) pairs, instead of true unification processes.

A similar criticism can be formulated against Sklar et al. (2012), who used CFS to show that masked sentences containing semantic anomalies (e.g. *"I ironed coffee"*) break through interocular suppression quicker than masked control sentences (e.g. "*I drank coffee"*), which they have interpreted as evidence for unconscious integration of different words into a sentence. As in the previous study, their results could be due to lexical differences between related (*drink-coffee*) and unrelated (*iron-coffee*) items, instead of unification mechanisms. Moreover, recently Sklar et al.'s findings failed to replicate (Rabagliati et al., 2018), and have been criticized based on methodological grounds as well (Shanks, 2017).

Overall, it is not clear whether previous work on semantic unification under reduced levels of awareness properly disentangled semantic unification and lexical retrieval effects. To the best of our knowledge, this is the first work that may control for this confound, as (i) in our study, we used sentences obtained by combining words that are not lexically related, and (ii) we directly compared masked sentences and single words within one experimental paradigm.

The claim that sentence processing is impaired under reduced awareness is also supported by studies performed when subjects were asleep and studies in patients with disorders of consciousness (DOC). Here, N400 effects are described as weaker, partial and delayed compared to wakefulness (Bastuji, Perrin, & Garcia-Larrea, 2002; Brualla, Romero, Serrano, & Valdizan, 1998; Daltrozzo, Claude, Tillmann, Bastuji, & Perrin, 2012; Davis et al., 2007; Ibáñez, López, & Cornejo, 2006; Rohaut et al., 2015; Steppacher, Kaps, & Kissler, 2016; Strauss & Dehaene, 2019). It has been argued that during sleep, there is decreased long-distance connectivity between brain regions (Boly et al., 2012; Massimini et al., 2005; Spoormaker, Gleiser, & Czisch, 2012; Tagliazucchi et al., 2013), and that the sleeping brain may still process semantic information, but in a purely feedforward manner (Strauss & Dehaene, 2019). In the vegetative state (no conscious awareness), it has been found that long-distance connectivity between frontal and temporal regions is disrupted (Boly et al., 2011). These findings are compatible with our hypothesis that long-distance feedback processing may play an important role in some sentence-level processes.

3.4.2. Visual masking as a tool to investigate feedback processing

One important assumption of this work is that visual masking selectively disrupts feedback processing between distant brain areas, while preserving feedforward processing. In many influential theories of consciousness, unconscious information seems to be processed mainly in a feedforward manner (Lamme & Roelfsema, 2000), while conscious processing is thought to be uniquely marked by dynamic recurrent interactions between distant brain regions (Dehaene & Changeux, 2011; Lamme, 2006). A highly-distributed fronto-temporo-parietal activation was found to be a correlate of conscious reportability (Del Cul et al., 2007), and long-distance feedback processing from frontal to temporal cortices was observed to be diminished in patients with disorders of consciousness (Boly et al., 2011). Further, previous research on visual perception showed that masking interferes with visual awareness by disrupting feedback processing from higher to lower visual areas, whereas feedforward processing is substantially preserved (Fahrenfort et al., 2007, 2017; Kovacs et al., 1995; Lamme, Zipser, & Spekreijse, 2002). Other studies showed that masking also disrupts long-distance feedback processing from frontal areas to higher visual areas (Del Cul et al., 2009).

Although these studies do not provide direct proof that masking impairs feedback processing between frontal and temporal areas, as predicted by the MUC model (Hagoort, 2017; Hultén et al., 2019), they strongly suggest that masking impairs long-distance feedback processing between many distant brain regions (potentially including frontal and temporal areas), while preserving feedforward processing. Therefore, an impairment of feedback between frontal and temporal areas due to masking seems a plausible consequence, although this should be confirmed by future studies.

Within this theoretical framework, when information is consciously processed in a global, recurrent network, it can also be maintained *ad libitum* in working memory (Baars & Franklin, 2003; Dehaene et al., 2006). Therefore, when feedback processing is impaired, working memory may also be impaired. Interestingly, previous studies have also shown that masking impairs working memory without directly affecting awareness of stimulus material (Blalock, 2013; Ricker & Sandry, 2018). The extent to which working memory and consciousness can be dissociated is debated (Soto & Silvanto, 2014). Future studies should address the question whether, and if so to what extent, working memory and awareness differentially affect unification processes. At the same time, the MUC model implements working memory, in the service of multi-word integration processes (Hagoort, 2017).

3.4.3. Residual levels of awareness in visual masking

Our behavioral results revealed that performance on masked single words, despite being poor, was above chance level, and thus participants may have been partially aware of the masked primes (possibly due to the fact that task instructions explicitly stated that in the masked conditions words were present). This is compatible with previous findings, showing that the N400 effect is absent when single words are presented in a fully unconscious fashion (Kang, Blake, & Woodman, 2011). Therefore, we do not claim that in our paradigm masked primes were unconscious. Still, visibility of masked and unmasked trials differed strongly, as revealed by accuracy in both the main and the discrimination task. Moreover, importantly, our results suggest that masked processing of sentences and single words may differ on a qualitative point of view. Namely, the N400 effect was present for masked single words, but not for masked sentences. If confirmed by future work, these qualitative differences would suggest that reducing stimulus visibility has a stronger effect on unification processes (fully abolishing it) compared to lexical retrieval processes (leaving it partly intact).

3.4.4. Differences between unification, multiple word processing and single word processing

One may argue that the differences between masked sentence and single word processing in our results are not truly qualitative, but only reflect higher difficulty of sentence processing compared to single word processing. Indeed, in the experiment reported in this chapter (compared to the experiment reported in Chapter 2) the N400 effects in the single word condition were stronger compared to the sentence condition (for both masking conditions). In our experimental paradigm, we aimed to minimize task differences between sentences and single words, for example by employing the same two-actor pictures in all conditions in the experiment reported in this chapter. However, one intrinsic limitation of our study (but potentially of all studies investigating sentence and single word processing) is that sentence and single word processing are hardly comparable, because task difficulty at the sentence level may be harder with respect to the single word level. In fact, the same holds for the factor masking: since the N400 effect is much larger for masked and unmasked stimuli, there is also more room for experimental modulations.

Our findings speak to a broad literature aiming to link ERP effects as the N400 and the P600 to lexical and/or unification processes. Whether the N400 effect reflects lexical or unification mechanisms is still a matter of debate (Baggio & Hagoort, 2011; Kutas & Federmeier, 2010; Lau et al., 2008). Recently, it has been proposed that the N400 effect indexes lexical retrieval, while the P600 (a centro-parietal distributed positivity often associated with syntactic violations, Hagoort et al., 1993), reflects unification (Brouwer, Crocker, Venhuizen, & Hoeks, 2017). In our results, we did not find any P600 effect in the sentence condition (not even in further uncorrected exploratory analyses, data not reported). Therefore, at least in our experimental paradigm, the N400 effect seems to reflect both unification and lexical retrieval processes.

It has been found that combinatorial operations simpler than sentence processing may occur under reduced levels of awareness (Armstrong & Dienes, 2013; Scott et al., 2018; van Gaal et al., 2014). Van Gaal et al. (2014) investigated the negation of valence by presenting masked negation-adjective pairs (e.g. *not-bad*), which formed incongruent combinations with a visible target (e.g. *murder*). They compared this condition with a congruent condition (e.g. *not-good murder*) and found an N400 effect . The paradigm employed by van Gaal et al. is comparable to our paradigm, in terms of both masking technique and timing of stimulus presentation, although the target was a picture in our study and a word in van Gaal et al.'s study. One may thus wonder why, in contrast to our studies, they did find an effect of masked multiple words processing. There may be two reasons for that, one methodological and one theoretical.

First, in the study by van Gaal et al. (2014) participants underwent a negation training in an experimental session before the main session (that took place on a different day), in which subjects were actively trained to either categorize the modifier-adjective combination as positive (e.g. *not-bad, very-good*), or negative (e.g. *not-good, very-bad*). This training likely increased the automaticity of the negation process, and established a lexical association between the negation and the adjective. Therefore, the likelihood of observing N400 effects in the following EEG session was also increased.

A second, theoretical, explanation comes from recent psycholinguistic theories, in which word retrieval and the application of simple syntactic rules are thought to share some neural resources (Jackendoff, 2007). Accordingly, chunks of syntactic structures (like negation+adjective or negation+noun combinations) are assembled in memory retrieval regions (LPTC), exploiting local processing within these areas, and stored there along with words. Later, these pre-assembled chunks are retrieved for unification operations and combined with other chunks in order to form larger structures, i.e. sentences (Hagoort, 2017). In this framework, the negation-adjective combinations investigated by van Gaal et al. (2014) differ from the sentence structures we focused on, which are higher in the syntactic hierarchy and may exploit different neural resources. The same is true for the findings of Armstrong & Dienes (2013), who investigated subliminal processing of negation using subjective threshold measurements.

Given the findings by van Gaal et al. (2014), it is unlikely that results of the masked sentence condition in the experiment reported in this chapter are fully explained by difficulties allocating attention to two words presented simultaneously, or by easier visibility of one prime word compared to multiple prime words. Taken together, our results and van Gaal et al.'s results suggest that masking may specifically disrupt sentence processing (unification), but not multiple word processing, although this is of course only indirect proof. The way awareness differentially modulates structures on different levels of the semantic and syntactic hierarchy should be further explored in future work.

3.4.5. Conclusion

In summary, our findings suggest that disrupting long-range feedback by means of visual masking may impair semantic unification, but not lexical retrieval. Since masking reduces visual awareness, this implies that single words may be processed under reduced awareness, whereas full awareness is required for semantic unification. If confirmed by future studies, our results may show that long-range feedback processing, potentially implying frontal and temporal areas, may be an important prerequisite of semantic unification, supporting a core prediction of the MUC model (Hagoort, 2017; Hultén et al., 2019; Snijders et al., 2009).

Acknowledgements

We thank Camilla Endrizzi for her valuable assistance with data acquisition.

4

Is feedback processing necessary for syntactic unification?

Abstract

Language combinatorial operations, here referred to as unification, take place in parallel at both the semantic and the syntactic level. Within the MUC (Memory, Unification and Control) model, semantic and syntactic unification are thought to require recurrent processing between the left inferior frontal cortex (LIFC) and the left posterior temporal cortex (LPTC). In previous work, we found that long-distance feedback processing, possibly involving frontal and temporal areas, may be crucial for semantic unification. Here, we investigate whether feedback processing is also required for syntactic unification. We employed a visual masking paradigm, by which we disrupted long-distance feedback processing, and investigated whether, under these conditions, syntactic unification mechanisms were preserved. We recorded event-related potentials (ERPs) while 40 participants performed a masked priming task, in which masked/unmasked primes (e.g. *he*) were followed by unmasked targets (e.g. *drives*), forming syntactically correct or incorrect combinations (*he drives* vs. **he drive*). This syntactic condition was compared with a semantic priming task, in which masked/unmasked primes and unmasked targets formed congruent or incongruent pairs (e.g. *winter-summer* vs. *winter-core*). In the unmasked condition, both semantic and syntactic stimuli triggered an N400 effect that, for semantic stimuli, was also followed by a late positivity. In the masked condition, no ERP effects were found. These results suggest that (i) long-distance feedback processing may be required for syntactic unification, although future studies should provide more direct and conclusive proof of this claim; (ii) task settings may strongly influence masked semantic priming at the single word level.

4.1. Introduction

Unification, according to the MUC (Memory, Unification and Control) model (Hagoort, 2005, 2013, 2017), refers to the combinatorial aspect of language. Unification is a hallmark of language processing across all representational domains, hence it is thought to take place in parallel at the syntactic, semantic and phonological level (Jackendoff, 2002, 2007). Semantic unification is defined as “the integration of word meaning into an unfolding representation of the preceding context” (Hagoort et al., 2009). Syntactic unification is defined as the combination of lexical items (words or chunks of structures, e.g. adjective+noun) retrieved from memory into larger structures (e.g. noun or verb phrases). This usually involves checking that agreement features (e.g. number, gender, person) of different lexical items match with each other[11]. Within the MUC framework, syntactic unification is realized in a dynamic interplay between the left inferior frontal cortex (LIFC) and the left posterior temporal cortex (LPTC, Snijders et al., 2009; Tyler et al., 2011), similarly to its semantic counterpart. Accordingly, syntactic unification may require feedback processing from LIFC to LPTC.

As noticed above, unification also occurs at the syntactic level. However, syntax and semantics cannot be reduced to each other (Adger, 2018; Chomsky, 1957), and semantic and syntactic processes are thought to be subserved by partially different brain mechanisms (Ferreira & Clifton, 1986; Friederici et al., 2000; Newman et al., 2003). It has been argued that semantic and syntactic unification rely on different regions within the LIFC, with dorsal and ventral areas that are specialized in syntactic and semantic unification, respectively (Hagoort & Indefrey, 2014). This suggests that semantic and syntactic unification should be tested separately.

In two electroencephalography (EEG) experiments (Mongelli, Meijs, van Gaal, & Hagoort, 2019), we tested the role of feedback processing in semantic unification and compared it to lexical retrieval, i.e. single word processing. We disrupted feedback mechanisms through visual masking and investigated whether, under these conditions, semantic unification mechanisms were preserved. Previous studies have shown that visual masking disrupts feedback processing between (distant) brain areas, while mostly preserving feedforward processing (Del Cul et al., 2009; Fahrenfort et al., 2007, 2017; Lamme & Roelfsema, 2000)[12]. We found that long-range feedback processing, potentially involving LIFC, is required for semantic unification, but not for lexical retrieval processes.

---

[11] For a more detailed account of semantic and syntactic unification, cf. Section 1.3.1 and 1.3.2 of the Introduction, respectively.

[12] For a more extensive discussion of this claim, cf. section 1.6 of the Introduction and the Discussion (section 3.4.2) of Chapter 3.

As argued above, semantic and syntactic unification are thought to be subserved by partially different mechanisms, hence they should be tested separately. Here, following up from our work on semantic unification, we investigated whether long-range feedback is involved in syntactic unification, similarly to semantic unification mechanisms. Unlike semantic priming, which has been extensively studied under different visibility conditions (Kouider & Dehaene, 2007), only a few studies specifically tackled syntactic processing under reduced levels of awareness. A few behavioral studies investigated masked syntactic priming at the single word level, for example comparing words of the same grammatical category with words of different grammatical categories (e.g. noun-noun vs. noun-verb), and these studies have observed that the repetition of the same grammatical category results in faster reaction times (RTs) compared to alternations in grammatical category (Ansorge et al., 2013; Berkovitch & Dehaene, 2019; Deutsch et al., 1998).

There is behavioral and neuroimaging evidence that syntactic processing under reduced levels of awareness may also be realized at the multiple word level (Batterink & Neville, 2013; Hung & Hsieh, 2015; Iijima & Sakai, 2014; Jiménez-Ortega, Espuny, de Tejada, Vargas-Rivero, & Martín-Loeches, 2017; Jiménez-Ortega et al., 2014; Pulvermüller & Shtyrov, 2003), even though evidence is mixed (Batterink et al., 2010). Some authors found that syntactic processing under reduced levels of awareness triggers an early left lateralized anterior negativity (ELAN/LAN) effect, while fully conscious syntactic processing uniquely evokes a P600 effect (Batterink & Neville, 2013; Jiménez-Ortega et al., 2014). Both ELAN/LAN and P600 have been observed in response to syntactic anomalies (Friederici, Pfeifer, & Hahne, 1993; Hagoort et al., 1993; Osterhaut & Holcomb, 1992). ELAN/LAN is thought to reflect automatic mechanisms mediating syntactic processing, whereas the P600 is elicited by more controlled mechanisms (Friederici, 2002), for example in response to the so-called garden path sentences (i.e. sentences in which, at critical points, the reader has to revise the structure initially followed – e.g. *The horse raced past the barn fell*). However, as we already noticed for masked semantic priming, experimental paradigms and techniques for reducing stimulus awareness strongly differ across studies.

In this study, we investigated whether long-range feedback is required for syntactic unification. As in the experiments described in Chapter 2 and 3, we disrupted feedback through visual masking and investigated whether, under these conditions, syntactic unification was preserved. To do so, we combined syntactic combinatorial processing and single word processing within the same paradigm. In an EEG experiment, masked/unmasked primes (e.g. *he* or *one*) were followed by unmasked targets (e.g. *drives* or *hat*), forming syntactically correct or incorrect combinations (*he drives* vs. **he drive*[13] or *one hat* vs. **one hats*). We compared these syntactically correct/incorrect combinations with single word pairs in a semantic priming task, in which masked/unmasked primes and unmasked targets formed congruent or incongruent combinations (e.g. *winter-summer* vs. *winter-core*).

In the unmasked condition, in which all words were clearly perceivable, we hypothesized that syntactic combinations would trigger a P600 effect, while semantic combinations would trigger an N400 effect. In the masked conditions, semantic combinations may also trigger an N400 effect, replicating previous findings (Deacon et al., 2000; Kiefer, 2002; Kiefer & Brendel, 2006; Kiefer & Spitzer, 2000). For masked syntactic combinations, there were two possibilities. If masked syntactic combinations would trigger an event-related potential (ERP) effect, for example the ELAN/LAN (Batterink & Neville, 2013; Jiménez-Ortega et al., 2014), this would suggest that long-range feedback processing is not required for syntactic unification. However, if no effects would be observed for masked syntactic combinations, we may conclude that long-range feedback is necessary for syntactic unification mechanisms, confirming our previous findings on semantic unification.

4.2. Material and Methods

4.2.1. Participants

48 subjects (28 females) participated in this study. Eight subjects presented drifts in the EEG signal due to hot weather conditions and hence a high temperature in the EEG lab. These eight participants were excluded from all analyses, before further hypothesis-driven inspection of their data. All subjects were right-handed native Dutch speakers, aged between 18 and 35, had normal or corrected-to-normal vision, no neurological history and were naive to the purpose of the experiment. Subjects gave written informed consent prior to participation, according to the Declaration of Helsinki. They received 25 euros or 2.5 research credits for their participation.

4.2.2. Stimuli

In the syntactic trials, we employed subject/verb pairs (e.g. *he drives*, in Dutch *hij rijdt*; see **Table 2** for a complete list of the verbs) and numeral/noun pairs (e.g. *one hat*, in Dutch *een muts*; see **Table 2** for a complete list of the nouns), forming syntactically correct or incorrect combinations (e.g. *he drives* or *one hat* vs. **he drive* or **one hats*, in Dutch *hij rijdt* or *een muts* vs. **hij rijden* or **een mutsen*).

---

[13] In linguistics, the star is used to mark an utterance considered as ungrammatical.

From now on, we will refer to these combinations as “syntactic-verb” and “syntactic-noun” pairs, respectively. In the syntactic-verb pairs, the subject was either the singular third-person pronoun *he* (in Dutch *hij*) or the plural first-person pronoun *we* (in Dutch *wij*). There were 30 verbs in total. In the syntactic-noun pairs, the numeral was either *one* (in Dutch *een*) or *two* (in Dutch *twee*). There were 30 nouns in total.

In the semantic trials, we employed prime/target pairs, either related or unrelated (e.g. *winter-summer* vs. *winter-core*, in Dutch *winter-zomer* vs. *winter-kern;* see **Table 1** for a complete list of the words). The lexical material included 30 nouns, divided as follows: 10 nouns were employed as targets and combined with 10 primes, either related or unrelated, thus forming 10 related and 10 unrelated prime/target pairs. Therefore, different word lists were employed for related primes, unrelated primes and targets. This means that target words never appeared as primes, and *vice versa*. On the contrary, the same words appeared as both masked and unmasked primes.

All nouns and verbs were 4-8 letters long, and matched for length and frequency within stimulus type (i.e. within semantic and syntactic trials) and across stimulus type (i.e. semantic vs. syntactic trials). Frequencies were extracted from SUBTLEX-NL, a database of Dutch word frequencies based on film and television subtitles (Keuleers, Brysbaert, & New, 2010)[14]. In all conditions, the two words were presented sequentially, i.e. one after the other.

The masks consisted of ten randomly chosen uppercase letters, which were slightly overlapping to increase the density of the mask. The space between the center of each letter was 10 pixels. Words and masks were presented in Arial lowercase font with a size of 20. Stimuli were presented in white against a black background. Participants were seated at a distance of approximately 70 cm from the computer screen.

4.2.3. Experimental design

The experiment was programmed using Presentation software (Neurobehavioral Systems, Albany, NY, USA). We employed a 2 (masking strength: masked or unmasked) x 2 (target congruency: congruent or incongruent) factorial design, separating syntactic and semantic stimuli. Note that the term “target congruency” includes both syntactic correctness (syntactic trials) and semantic relatedness (semantic trials). In both syntactic and semantic blocks, each block included 120 trials and lasted approximately 5 minutes. In total, there were 480 trials in the

---

[14] For further details about the measure employed to calculate word frequencies, as well as for statistical comparisons, cf. Table 1 and 2.

semantic trials and 960 trials in the syntactic trials, equally divided across syntactic-verb and syntactic-noun trials (so 480 trials in each condition). Each block included 50% masked and 50% unmasked trials, randomly mixed within blocks.

In masked trials, we presented a fixation cross (300 ms), a blank screen (200 ms), a first mask (67 ms), a prime (33 ms), a second mask (67 ms), a target (500 ms) and a fixation cross (700 ms). After the fixation cross, an answer screen with the options *match/no match* (in Dutch: *wel match/geen match*) appeared (see **Figure 4.1A** and **4.1C** for examples of the trial structure). The position of the match answer (left or right) was randomized across trials. In unmasked trials, we presented a fixation cross (300 ms), a blank screen (200 ms), a first blank (67 ms), a prime (33 ms), a second blank (67 ms), a target (500 ms) and a fixation cross (700 ms). Trials had a duration of 1867 ms.

Participants were instructed to respond to the target only after the answer screen appeared. They had to indicate whether the target matched or did not match with the prime by pressing either a left or a right key on the keyboard with their left or right hand, respectively. In order to make the task meaningful in the masked condition, participants were told that each block included “easy” and “difficult” trials. In the difficult trials, words were “hidden”, which made them very hard to be read. However, they had to try their best to respond correctly. Therefore, participants knew that prime words were presented in the masked condition, but they could not perceive them clearly. Note that in all conditions participants needed to discriminate both words in order to perform the match/no match task correctly. Therefore, in this experiment the main task also allowed to determine the visibility of the prime.

There was no speed stress on the response. Each block included 50% congruent and 50% incongruent trials, randomly mixed within blocks. The interval between trials varied between 750 and 1250 ms, drawn from a random distribution. At the end of each block, feedback was provided on participants’ accuracy, for both masked and unmasked trials.

4.2.4. Procedure

The experiment consisted of one main EEG session. Before starting the EEG recording, participants were introduced to both task and stimuli and performed three practice blocks (one per block type). Next, participants performed the main task (12 blocks: 4 syntactic-verb, 4 syntactic-noun and 4 semantic) and EEG was recorded. Block order, both in the practice and in the main task, was randomized across participants.

4.2.5. Electroencephalographic measurements

The electroencephalogram was recorded continuously from 70 active electrodes using a BioSemi ActiveTwo System. 64 of these electrodes were mounted on a cap. Two reference electrodes were placed on the left and right ear lobe. Blinks were monitored through two electrodes placed above and below the pupil of the left eye. Horizontal eye movements were monitored through two electrodes placed on the lateral canthi next to the left and right eye. Each electrode recording eye movements was referenced to its counterpart.

The EEG signal was recorded with a sampling rate of 512 Hz, then resampled at 500 Hz[15] and filtered offline with a high-pass filter of 0.1 Hz and a low-pass filter of 40 Hz. All electrode sites were re-referenced offline to the average of left and right ear lobes and epoched from -0.667 (i.e. the beginning of a trial) to +1.2 s (i.e. the end of a trial; the answer screen was presented 1.2 seconds after the onset of the target) surrounding each trial. All ERPs were time-locked to the target, i.e. second word, presentation. Next, trials were visually inspected and those containing artefacts not related to blinks were manually removed. Note that visual inspection was blind to the conditions of the experiment. Deleted channels were reconstructed based on a nearest neighbor approach. Independent component analysis (ICA) was computed and components containing blink/oculomotor artefacts were removed from the data. The blank interval before the first mask (pre-target interval: 367-167 ms before target) was employed as a baseline.

4.2.6. Statistical analyses

Behavioral analyses (repeated measures ANOVAs and paired t-tests) were performed in MATLAB. For our ERP analyses, all preprocessing steps were conducted with Fieldtrip (Oostenveld et al., 2011). ERP statistical analyses were performed using a combination of Fieldtrip and MATLAB (The Mathworks, Natick, MA, USA) scripts. The ERP analysis procedure, which is the same employed for our previous experiments, is reported below.

In the unmasked condition, we expected to find N400 and P600 effects in semantic and syntactic stimuli, respectively. As already noticed previously, the N400 typically has a centro-parietal topography and is maximum in a time window of ~250-500 ms, although the exact timing is quite variable (Kutas & Federmeier, 2010; Lau et al., 2008). The N400 effect has been consistently observed in re-

---

[15] Resampling was performed in order to keep the same sampling rate across all experiments performed in this thesis, since experiments described in Chapter 2, 3 and 5 were performed at a sampling rate of 500 Hz. The reason for this difference is that the experiments reported in Chapter 2, 3 and 5 were performed at the Max Planck Institute for Psycholinguistics in Nijmegen, whereas the experiment reported in this chapter was performed at the University of Amsterdam.

sponse to semantic anomalies and violations, even if it has also been linked to many other cognitive processes. Similar considerations hold for the P600. The P600 usually peaks at centro-parietal electrodes, within a typical time window of 500-700 ms, and the P600 effect is usually associated with the processing of syntactic anomalies. However, stimulus and task-dependent variability has been observed (Gouvea, Phillips, Kazanina, & Poeppel, 2010). Therefore, for both N400 and P600 effects, we mainly focused on the polarity of the effect, that is, we expected a negative and positive difference between incongruent and congruent trials, respectively.

First, we performed cluster-based permutation tests (Maris & Oostenveld, 2007) on the time window 0-1.2 s from target (i.e. second word) onset to isolate significant ERP effects related to syntactic violation or semantic incongruency (contrast incongruent vs. congruent, computed separately for semantic and syntactic stimuli). A minimum of two neighboring electrodes had to pass the threshold of $p<0.05$ to form a cluster. Cluster-based correction was based on 10000 iterations. This Monte-Carlo method generated a nonparametric estimate of the p-value representing the statistical significance of the originally identified cluster. This analysis isolated significant effects as clusters in time and space. To visualize the evolution of significant clusters, we divided the time period (0-1.2 s) in 12 equal bins of 100 ms and plotted for each bin (i.e. 0-100, 100-200, etc.) all electrodes that were significant at least 50% of the time-window (as an example, cf. **Figure 4.2A**).

Next, for follow-up analyses we isolated the exact time window and channels where the effects were strongest. To do so, the onset and offset of a cluster were defined as the time period around the maximum difference where the difference did not drop below 50% of this maximum and where at least one channel showed a significant effect. We then selected the 10 channels within the cluster that showed the largest effect in this time window (for a similar procedure, cf. Mongelli et al., 2019 and Meijs et al., 2018). The resulting regions of interest (ROI) and time windows were then used for subsequent analyses, including all the relevant factors. Note that, as a “sanity check”, all analyses were also performed on central and posterior ROIs, defined based on previous literature on the N400 (Kutas & Federmeier, 2010) and the P600 (Gouvea et al., 2010), respectively. These supplementary analyses led to the same conclusions.

4.3. Results

Our goal was to investigate whether syntactic unification requires neural feedback between distant brain areas. We addressed this issue by interfering with feedback processing by means of visual masking, and comparing masked and unmasked processing of syntactic unification vs. lexical retrieval processes.

4.3.1. Behavior

Here, we tested how masking strength affected participants' accuracy. We observed that masking reduced participants' accuracy (main effect of masking strength: $F_{1,39}>1000$, $p<0.001$), but performance was not modulated by stimulus type (syntactic vs. semantic, interaction masking strength x stimulus type: $F_{1,39}=1.38$, $p=0.246$). Within syntactic stimuli, participants' accuracy did not differ across syntactic-verb and syntactic-noun trials (interaction masking strength x stimulus type: $F_{1,39}=1.71$, $p=0.200$).

For both syntactic and semantic stimuli, the masked and unmasked conditions differed significantly, accuracy being significantly lower in the masked condition than in the unmasked condition (syntactic stimuli: $t_{39}=44.27$, $p<0.001$; semantic stimuli: $t_{39}=36.72$, $p<0.001$. **Figure 4.1B** and **4.1D**). In the unmasked condition, subjects performed well and strongly above chance (syntactic stimuli: $t_{39}=51.13$, $p<0.001$, 93% correct; semantic stimuli: $t_{39}=49.72$, $p<0.001$, 94% correct. **Figure 4.1B** and **4.1D**). Performance in the masked condition was much poorer and numerically close to chance-level, although statistically above chance level for both syntactic and semantic stimuli (syntactic stimuli: $t_{39}=2.62$, $p=0.012$, 51.19% correct; semantic stimuli: $t_{39}=5.00$, $p<0.001$, 53% correct. **Figure 4.1B** and **4.1D**).

Overall, behavioral results showed that masked and unmasked trials were perceived very differently, as revealed by much lower accuracy in the masked compared to the unmasked condition. However, accuracy was above chance level in the masked condition as well. This suggests that, as in the previous experiments, participants may have been partially aware of masked primes (although we cannot be sure). Therefore, as in our previous studies, masking created a quantitative difference in visibility rather than a qualitative difference (we do not consider the masked stimuli as completely unconscious)[16].

---

[16] For a more extensive discussion of this issue, cf. the Discussion (section 3.4.3) of Chapter 3.

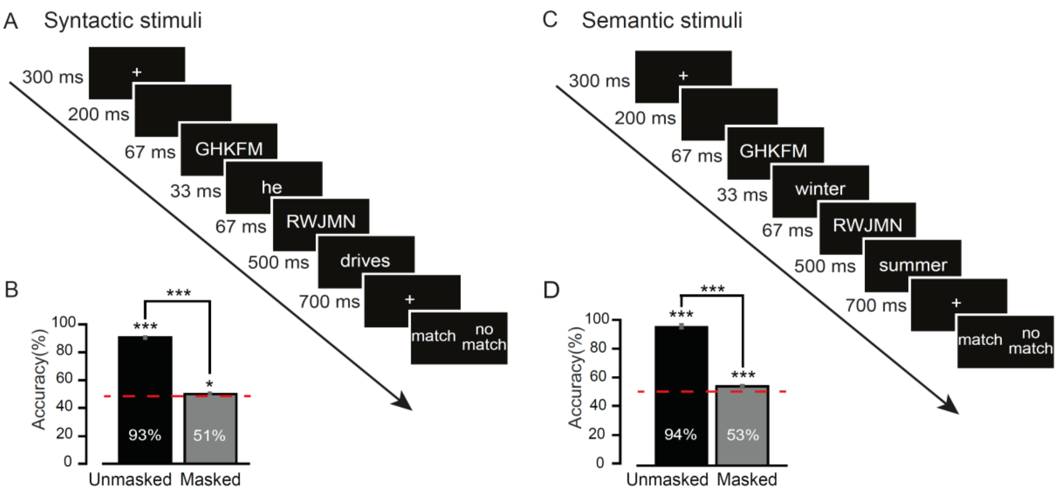

Figure 4.1: Paradigm and behavioral results. (A) Trial structure for masked syntactic combinations. One prime (e.g. *he*) was followed by an unmasked target (e.g. *drives*), forming syntactically correct or incorrect combinations (*he drives* vs. **he drive*). In the figure, a syntactically correct trial is represented. Participants performed a match/no match task. **(B)** Participants' accuracy for unmasked (black) and masked (grey) syntactic trials separately. Error bars represent between-subject SEM. **(C)** Trial structure for masked semantic pairs. One prime (e.g. *winter*) was followed by an unmasked target (e.g. *summer*), forming congruent or incongruent pairs (e.g. *winter-summer* vs. *winter-core*). In the figure a congruent trial is represented. **(D)** Participants' accuracy for unmasked (black) and masked (grey) semantic trials separately. Error bars represent between-subject SEM.

4.3.2. ERPs

In this experiment, we investigated whether a reduction in awareness through visual masking affected syntactic unification and lexical retrieval processes. To this aim, we contrasted incongruent and congruent trials using cluster-based permutation testing, correcting for multiple comparisons across both time (0-1.2 s) and (electrode) space (see **Figure 4.2A** and Methods section, Maris & Oostenveld, 2007).

We will first report the analyses for syntactic stimuli. When isolating significant effects (incongruent - congruent) as clusters in time and space, we found a significant negative cluster over central electrodes from 398-594 ms after target onset and peaking at 496 ms (see **Figure 4.2A**; p-value of the cluster between 398-594 ms: p<0.001). Next, we investigated how this ERP effect, which looked like a typical N400 effect, was modulated by masking strength. To this aim, within syntactic stimuli we performed repeated measures ANOVAs on the ERP time window found with the cluster-based permutation procedure, with two factors: masking strength (masked/unmasked), and prime/target congruency (congruent/incongruent). We found that the N400 effect (main effect of congruency: $F_{1,39}=44.58$, $p<0.001$) was larger for unmasked than for masked trials (interaction masking strength x congruency: $F_{1,39}=53.88$, $p<0.001$). There was no difference between syntactic-verb and syntactic-noun trials, as the 3-way interaction between masking strength, congruency and stimulus type (syntactic-verb or syntactic-noun) was not significant ($p=0.433$). In post-hoc analyses, we tested the ERP effects for masked and unmasked trials. In unmasked syntactic stimuli, incongruent trials triggered a larger N400 compared to congruent trials ($t_{39}=9.17$, $p<0.001$. **Figure 4.2B**). On the contrary, in masked syntactic stimuli, there was no difference between congruent and incongruent trials ($p=0.636$. **Figure 4.2C**).

Next, we focused on the semantic stimuli. Similarly to syntactic stimuli, in the cluster-based analysis we found a negative difference, which was significant over central electrodes from 318-642 ms after target onset and peaking at 462 ms (see **Figure 4.3A**; p-value of the cluster between 318-642 ms: $p<0.001$). This negative difference was followed by a late positive difference, which was significant over centro-parietal electrodes from 1062-1200 ms after target onset and peaking at 1182 ms (see **Figure 4.3A**; p-value of the cluster between 1062-1200 ms: $p=0.022$). As previously reported for syntactic stimuli, within semantic stimuli we now performed repeated measures ANOVAs on the ERP time windows found with the cluster-based permutation procedure, with two factors: masking strength (masked/unmasked), and prime/target congruency (congruent/incongruent). We found that the N400 effect (main effect of congruency: $F_{1,39}=34.89$, $p<0.001$) was larger for unmasked than masked trials (interaction masking strength x congruency: $F_{1,39}=56.22$, $p<0.001$). The late positivity (main effect of congruency: $F_{1,39}=26.51$, $p<0.001$) was also larger for unmasked compared to masked trials (interaction masking strength x congruency: $F_{1,39}=28.02$, $p<0.001$). In post-hoc analyses, we tested the ERP effects for masked and unmasked semantic trials. In the unmasked condition, there was a difference between congruent and incongruent trials, both in the N400 and in the late positive time window (N400 effect: $t_{39}=9.38$, $p<0.001$; late positive effect: $t_{39}=-6.06$, $p<0.001$. **Figure 4.3B**). On the contrary, no difference was found for masked trials, neither in the N400 nor in the late positive time window (N400 effect: $p=0.482$; late positive effect: $p=0.867$. **Figure 4.3C**).

In summary, in this experiment we found an N400 effect in unmasked semantic pairs and, surprisingly, also in unmasked syntactic combinations. In unmasked semantic pairs, this N400 effect was followed by a late positivity. On the contrary, in the masked condition we found no ERP effects, neither in the syntactic condition nor in the semantic condition.

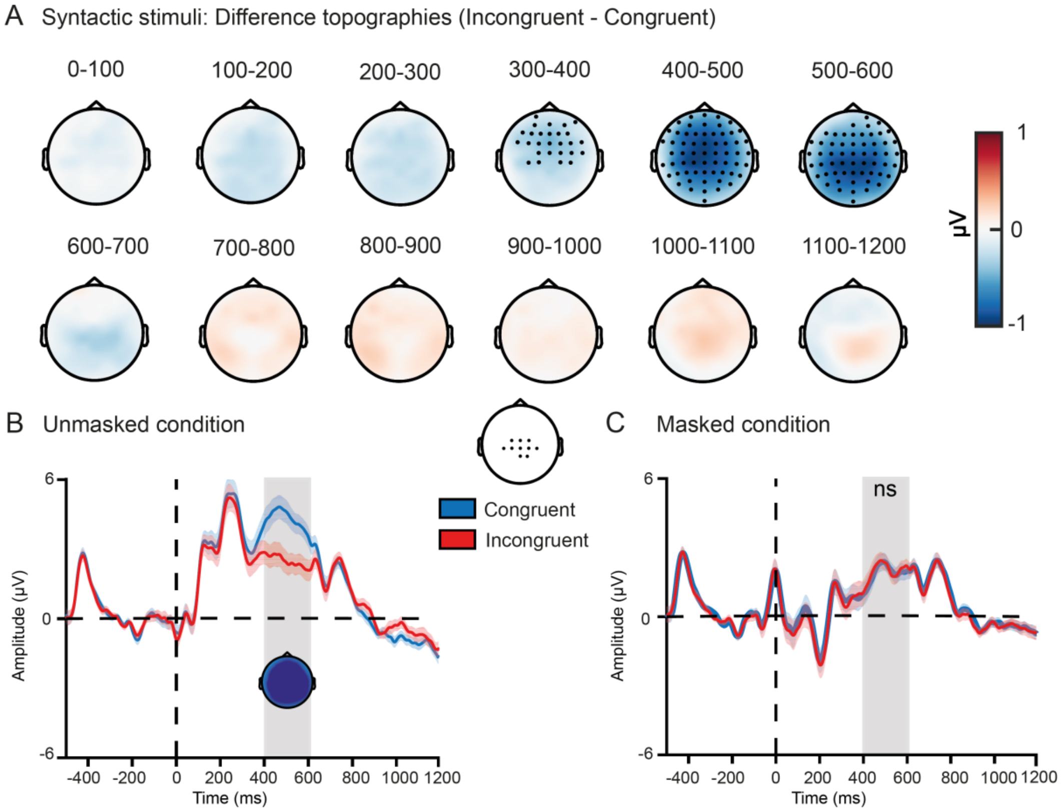

Figure 4.2: ERP effects for syntactic stimuli. (A) Topographic maps of the difference between syntactic incongruent and congruent trials over time (0 = target onset). Cluster-based permutation tests were used to isolate the significant events, while correcting for multiple comparisons across time and (electrode) space. On each head map, channels with a significant effect for at least 50% of its time window are highlighted. **(B)** ERPs for a central region of interest (see inset) for congruent (blue) and incongruent (red) unmasked syntactic trials. **(C)** ERPs for a central region of interest (see inset) for congruent (blue) and incongruent (red) masked syntactic trials. Inset represents the channels within the cluster that

showed the largest effect in the time window 398-594 ms. In both figures 4.2B and 4.2C shaded blue and red areas around the wave form indicate between-subject SEM. Time 0 represents target onset. Shaded grey areas highlight the time window of interest for the N400 effect (398-594 ms). All headmaps are scaled from -1 to 1 microvolts.

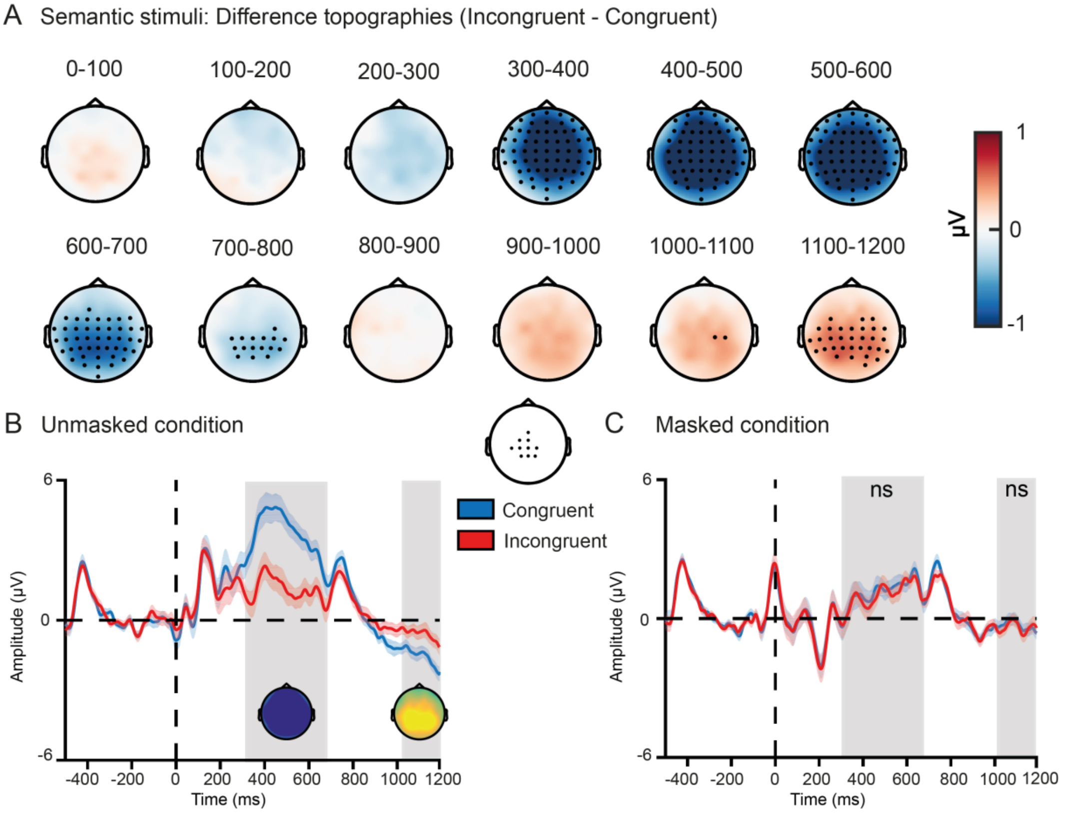

Figure 4.3: ERP effects for semantic stimuli. (A) Topographic maps of the difference between semantic incongruent and congruent trials over time (0 = target onset). Cluster-based permutation tests were used to isolate the significant events, while correcting for multiple comparisons across time and (electrode) space. On each head map, channels with a significant effect for at least 50% of its time window are highlighted. **(B)** ERPs for a central region of interest (see inset) for congruent (blue) and incongruent (red) unmasked semantic trials. Note that the late positive effect shown in the headmap was tested on a different, centro-parietal region of interest obtained with the cluster-based permutation procedure (see Results). **(C)** ERPs for a central region of interest for congruent (blue) and incon-

gruent (red) masked semantic trials. Inset represents the channels within the negative cluster that showed the largest effect in the time window 318-642 ms. In both figures 4.3B and 4.3C shaded blue and red areas around the wave form indicate between-subject SEM. Time 0 represents target onset. Shaded grey areas highlight the time window of interest for the N400 effect (318-642 ms) and the late positive effect (1062-1200 ms). All headmaps are scaled from -1 to 1 microvolts.

4.4. Discussion

In this study, we explored the mechanisms subserving syntactic unification and compared them to lexical retrieval processes. Long-range feedback from the left inferior frontal cortex (LIFC) to the left posterior temporal cortex (LPTC) is thought to be crucial for unification processes (both at the semantic and the syntactic level), but not for lexical retrieval (Hagoort, 2005, 2013, 2017; Tyler et al., 2011). In two previous studies, described in Chapters 2 and 3, we tested this hypothesis and found that long-range feedback, potentially involving LIFC, seems to be required for semantic unification. Our findings showed that, when disrupting feedback with visual masking, semantic unification mechanisms were impaired, while lexical retrieval processes were partly preserved. Here, we aimed to extend our findings to syntactic unification. Following the same logic, we interfered with feedback through masking, which is thought to disrupt long-range feedback processing (Fahrenfort et al., 2007, 2017; Lamme & Roelfsema, 2000), likely also involving frontal areas (Del Cul et al., 2009).

In an EEG experiment, we presented masked/unmasked primes (e.g. *he* or *one*) followed by unmasked targets (e.g. *drives* or *hat*), forming syntactically correct or incorrect combinations (*he drives* vs. **he drive* or *one hat* vs. **one hats*). We compared these syntactically correct/incorrect combinations with word pairs in a semantic priming task, in which masked/unmasked primes and unmasked targets formed congruent or incongruent combinations (e.g. *winter-summer* vs. *winter-core*). Participants were asked whether the words matched together or not (match/no match task).

Behaviorally, performance on the matching task was higher in the unmasked compared to the masked condition, showing that masking strongly reduced prime visibility. In EEG, for all unmasked combinations (syntactic and semantic) we found an N400 effect. In semantic stimuli, this N400 effect was followed by a late positivity, possibly reflecting a general taxing of cognitive resources after a semantic association problem (Hagoort, Wassenaar, & Brown, 2003). On the contrary, we did not find any ERP effects in the masked condition.

In the case of unmasked syntactic stimuli, the pattern of results was quite anomalous, since we expected syntactic violations to trigger a typical P600 effect, as shown by several previous studies (e.g. Gouvea et al., 2010; Hagoort et al., 1993; Osterhaut and Holcomb, 1992). A tentative explanation for the absence of a P600 effect is that, in our experiment, participants were required to perform a generic match/no match task, without being explicitly tested on grammatical correctness. The appearance of N400 effects in response to syntactic violations has been previously documented in aphasic patients (Hagoort et al., 2003). However, to the best of our knowledge, this question has never been investigated in healthy subjects.

The absence of ERP effects for syntactic combinations when all words are masked may indicate that syntactic unification cannot be performed in absence of feedback processing. However, since we did not find an effect for the semantic condition either, we cannot be sure that this null result was really driven by the combinatorial nature of syntactic stimuli or that, instead, our paradigm simply could not capture any effect driven by masked words.

We reasoned that the absence of an effect for masked semantic stimuli may be caused by two possible factors. First, we employed different word lists for primes and targets. It has been argued that masked priming only occurs when words appear as both primes and targets, thus forming automatic word associations that do not need to be processed at the semantic level (Abrams & Greenwald, 2000; Damian, 2001). The existence of genuine masked semantic priming effects, independent from learned stimulus-response mappings, remains debated (Avneon & Lamy, 2019; Kouider & Dehaene, 2007; Kunde, Kiesel, & Hoffmann, 2005; Van den Bussche, Van den Noortgate, et al., 2009; Van Opstal, Reynvoet, & Verguts, 2005a, 2005b). A less controversial claim is that automatic stimulus-response mapping enhances masked priming effects (Van den Bussche, Van den Noortgate, et al., 2009).

The second factor may be related to specific features of our task. In our task, we employed a match/no match decision, which implies that participants were asked to process both words in each pair and judge their relationship. However, in most commonly used masked priming paradigms, participants are only tested on the target, for example through lexical decision tasks (word/nonword, e.g. Kiefer, 2002; Kiefer & Spitzer, 2000), valence categorization (positive/negative, e.g. Abrams et al., 2002; van Gaal et al., 2014), or animacy categorization tasks (animate/inanimate, e.g. Ortells et al., 2016). It has been found that specific task settings may affect the extent and type of (neural) processing that presented words induce (Kiefer & Martens, 2010; Van den Bussche, Van den Noortgate, et al., 2009). For example, perceptual tasks (e.g. decision on open/close shape of first and last letter) have been shown to reduce the size of observed N400 effects compared to semantic tasks (e.g. animacy categorization task, Kiefer & Martens, 2010). Nevertheless, to the best of our knowledge, no previous studies have focused on the question how masked priming is affected by tasks involving either decisions on both prime and target or decisions on the target only.

To overcome these limitations, and to test some of our post-hoc hypotheses on task influence on N400/P600 effects, we performed a follow-up experiment with three main changes to the design and stimulus material. First, for syntactic stimuli, in task instructions participants were explicitly asked to judge the grammatical correctness of the short combinations. Second, in semantic pairs, all words appeared as both primes and targets, thus creating automatic stimulus-response associations between words within a pair. Third, in semantic pairs, only targets were task-relevant, because subjects had to perform an animacy categorization task on the target (the prime was therefore task-irrelevant). We hypothesized that these changes in the semantic priming paradigm may enhance masked semantic processing. Observing an ERP effect in the semantic case, but not in the syntactic case, for masked stimuli is crucial because only then we can conclude that there is a crucial role of feedback processing in syntactic unification. Issues related to both this study and its follow-up will be jointly discussed in the Discussion section of the following chapter.

Acknowledgements

We thank Nutsa Nanuashvili for her valuable assistance with data acquisition.

4.5. Tables

Semantic stimuli			
Targets	**Frequency-Lg10WF**	**Word length**	**Translation**
schaap	2,4579	6	sheep
muziek	3,6721	6	music
winter	2,9908	6	winter
hemel	3,7085	5	heaven
wind	3,345	4	wind
vork	2,3579	4	fork
stekels	1,3617	7	spines
verf	2,8021	4	paint
winst	2,9763	5	gain
draad	2,7657	5	string
Mean	2,843	5,200	
SD	0,692	1,032	
Related primes	**Frequency-Lg10WF**	**Word length**	**Translation**
herder	2,415	6	shepherd
ritme	2,5888	5	rhythm
zomer	3,2735	5	summer
ster	3,2822	4	star
storm	3,1126	5	storm
lepel	2,3424	5	spoon
egel	1,415	4	hedgehog

kwast	1,8808	5	brush
verlies	3,3318	7	loss
naald	2,5717	5	needle
Mean	2,621	5,100	
SD	0,644	0,875	
Unrelated primes	**Frequency-Lg10WF**	**Word length**	**Translation**
preek	2,4942	5	sermon
vorst	2,2788	5	freeze-monarch
kern	2,6085	4	core
lijn	3,478	4	rope
basis	3,1816	5	basis
stier	2,6243	5	bull
villa	2,5224	5	villa
saldo	1,6628	5	balance
suiker	2,98	6	sugar
heks	3,0686	4	witch
Mean	2,689	4,800	
SD	0,515	0,632	
	Targets vs. Related primes	**Targets vs. Unrelated primes**	**Related vs. Unrelated primes**
Frequency	p=0,171	p=0,519	p=0,675
Word length	p=0,832	p=0,343	p=0,193

Table 1. List of semantic stimuli (column 1), with relative frequency (column 2), length (column 3) and English translation (column 4). Mean and standard

deviation (SD) of word frequencies and word length are reported in column 2 and 3, respectively. 10 nouns were employed as targets and combined with 10 primes, either related or unrelated, thus forming 10 related and 10 unrelated prime/target pairs. Different word lists were employed for related primes, unrelated primes and targets, hence target words never appeared as primes, and *vice versa*. Frequencies were extracted from SUBTLEX-NL, a database of Dutch word frequencies based on film and television subtitles (Keuleers et al., 2010). Our measure for frequency was Lg10WF, i.e. the logarithm to the base 10 of FREQcount+1, where FREQcount is the number of times the word appeared in the corpus (i.e. on the total of 43.8 million words). According to Keuleers et al. (2010), calculating the log frequency on the raw frequencies is the most straightforward transformation, because it allows researchers to give words that are not in the corpus a value of 0. All words were matched for length and frequency (p-values reported in the table).

Syntactic stimuli - Verbs	**Frequency-Lg10WF**	**Word length**	**Translation**
rijden	3,817	6	drive
niezen	1,9294	6	sneeze
lezen	3,6735	5	read
zingen	3,4573	6	sing
klagen	2,937	6	complain
bijten	2,8445	6	bite
rennen	3,5047	6	run
raden	3,0917	5	guess
kopen	3,7569	5	buy
roken	3,2833	5	smoke
lopen	3,9863	5	walk
verven	2,29	6	paint
winnen	3,7074	6	win
bidden	3,2071	6	pray

huilen	3,3775	6	cry
rijdt	3,3294	5	drives
niest	1,4314	5	sneezes
leest	3,0465	5	reads
zingt	2,8639	5	sings
klaagt	2,4472	6	complains
bijt	2,8733	4	bites
rent	2,6893	4	runs
raadt	2,3502	5	guesses
koopt	2,9795	5	buys
rookt	2,7292	5	smokes
loopt	3,7778	5	walks
verft	1,4472	5	paints
wint	3,3212	4	wins
bidt	2,2253	4	prays
huilt	2,7356	5	cries
Mean	2,970	5,233	
SD	0,665	0,678	
Syntactic stimuli - Nouns	**Frequency-Lg10WF**	**Word length**	**Translation**
kast	3,1189	4	wardrobe
kruk	2,0531	4	stool
hand	3,9417	4	hand
stoel	3,3502	5	chair
trein	3,5051	5	train
muts	2,2923	4	hat

jurk	3,3872	4	dress
bank	3,6042	4	bench
kers	1,8573	4	cherry
hond	3,8678	4	dog
nicht	3,0022	5	niece
agent	3,9117	5	agent
jurist	2,1903	6	lawyer
rat	2,9978	3	rat
wesp	1,4472	4	wasp
kasten	2,0792	6	wardrobes
krukken	1,8692	6	stools
handen	3,9729	6	hands
stoelen	2,6911	7	chairs
treinen	2,444	7	trains
mutsen	1,1761	6	hats
jurken	2,4829	6	dresses
banken	2,6222	6	benches
kersen	2,017	6	cherries
honden	3,3514	6	dogs
nichten	2,0828	7	nieces
agenten	3,4293	7	agents
juristen	1,8633	8	lawyers
ratten	2,8854	6	rats
wespen	1,1761	6	wasps
Mean	2,688	5,366	
SD	0,834	1,245	

	Semantic stimuli vs. Syntactic stimuli (Verbs)	**Semantic stimuli vs. Syntactic stimuli (Nouns)**	**Syntactic stimuli (Verbs) vs. Syntactic stimuli (Nouns)**
Frequency	p=0,120	p=0,875	p=0,124
Word length	p=0,325	p=0,299	p=0,625

Table 2. List of syntactic stimuli (nouns and verbs, column 1), with relative frequency (column 2), length (column 3) and English translation (column 4). Mean and standard deviation (SD) of word frequencies and word length are reported in column 2 and 3, respectively. Verbs were combined with the singular third-person pronoun *he* (in Dutch *hij*) or the plural first-person pronoun *we* (in Dutch *wij*), forming syntactically correct or incorrect combinations (e.g. *he drives* vs. **he drive*, in Dutch *hij rijdt* vs. **hij rijden* or *we drive* vs. **we drives*, in Dutch *wij rijden* vs. **wij rijdt*). Nouns were combined with the numeral *one* (in Dutch *een*) or *two* (in Dutch *twee*), forming syntactically correct or incorrect combinations (e.g. *one hat* vs. **one hats*, in Dutch *een muts* vs. **een mutsen* or *two hats* vs. **two hat*, in Dutch *twee mutsen* vs. **twee muts*). Our measure for frequency was Lg10WF (see legend of Table 1 for further details). All words were matched for length and frequency (p-values reported in the table).

5

Is feedback processing necessary for syntactic unification? Task-related effects on syntactic and semantic processing

Abstract

What is the role of feedback processing in syntactic unification? The Memory, Unification and Control (MUC) model postulates that feedback from the left inferior frontal cortex (LIFC) is required for unification, both at the semantic and the syntactic level, but not for single word processing. In a recent experiment, we investigated the role of feedback in syntactic unification. With electroencephalography (EEG), we compared syntactic unification and single word processing in a masked priming paradigm. Visual masking is thought to disrupt feedback between distant brain areas. Masked/unmasked primes (e.g. *he*) were followed by unmasked targets (e.g. *drives*), forming syntactically correct or incorrect combinations (*he drives* vs. **he drive*). This syntactic condition was compared with a semantic condition, with masked/unmasked primes and unmasked targets forming congruent or incongruent pairs (e.g. *winter-summer* vs. *winter-core*). Participants performed a match/no match task. In the unmasked condition, we found an N400 effect in the semantic condition and, surprisingly, also in the syntactic condition. We found no effect in the masked condition, hence leaving unanswered whether unification impairment was specifically caused by feedback disruption. In the present follow-up experiment, we aimed to clarify these issues by (i) modifying the task in the syntactic condition; and (ii) by modifying prime novelty and task in the semantic condition. In the unmasked condition, we found a P600 effect for syntactic combinations and a positivity for semantic pairs. This positivity was also present for masked semantic pairs. No effect was found for masked syntactic combinations. Overall, these findings suggest that (i) feedback processing is required for syntactic unification, but not for single word processing; and (ii) that the specific task parameters strongly influence the event-related potential (ERP) effects that are observed when studying both syntactic and semantic processing.

5.1. Introduction

Unification, which refers to the combinatorial aspect of language, takes place at both the semantic and syntactic level. The Memory, Unification and Control (MUC) model predicts that feedback processing from the left inferior frontal cortex (LIFC) to the left posterior temporal cortex (LPTC) is crucial for unification, whereas single word processing only relies on feedforward processing (Hagoort, 2017; Hultén et al., 2019; Snijders et al., 2009; Tyler et al., 2011).

In previous work, we tested the importance of feedback processing for semantic unification (Mongelli et al., 2019). We employed visual masking, which is thought to impair feedback processing between distant brain areas (Fahrenfort et al., 2007, 2017; Lamme & Roelfsema, 2000), potentially involving frontal regions (Del Cul et al., 2009). In a masked semantic priming paradigm, we disrupted feedback and compared electroencephalography (EEG) signatures of semantic unification and single word processing. We found that masking selectively disrupts semantic unification mechanisms, while preserving single word processing.

Syntax is not reducible to semantics, and *vice versa* (Adger, 2018; Chomsky, 1957). Moreover, semantic and syntactic processes are thought to rely on partially different brain mechanisms (Ferreira & Clifton, 1986; Friederici et al., 2000; Newman et al., 2003). It has been argued that semantic and syntactic unification are subserved by different regions within the LIFC, with dorsal and ventral areas that are specialized in syntactic and semantic unification, respectively (Hagoort & Indefrey, 2014). Overall, there is both theoretical and empirical evidence suggesting that brain mechanisms underlying syntactic and semantic unification should be tested separately.

Following the same logic of the previous study, in a recent EEG experiment we investigated syntactic unification by comparing it with single word processing. In a syntactic priming paradigm, masked/unmasked primes (e.g. *he* or *one*) were followed by unmasked targets (e.g. *drives* or *hat*), forming syntactically correct or incorrect combinations (*he drives* vs. **he drive*[17] or *one hat* vs. **one hats*). This syntactic condition was compared with a semantic condition, with masked/unmasked primes and unmasked targets forming congruent or incongruent pairs (e.g. *winter-summer* vs. *winter-core*). In both the syntactic and the semantic condition, participants were asked to judge if the word combinations matched together or not (match/no match task).

Our results in the unmasked condition showed that both semantic and syntactic stimuli triggered an N400 effect, i.e. a negative event-elated potential (ERP) typically observed in response to semantic incongruencies (Kutas & Federmeier,

---

[17] In linguistics, the star is used to mark an utterance considered as ungrammatical.

2010; Lau et al., 2008). These results were quite anomalous for syntactic stimuli, as syntactic anomalies typically induce a P600 effect (Hagoort et al., 1993; Osterhaut & Holcomb, 1992). To the best of our knowledge, N400 effects induced by syntactic violations have only been documented in aphasic patients with deficits in grammar comprehension (Hagoort et al., 2003). As a post-hoc explanation, we reasoned that these unexpected findings could be task-driven, since we performed a generic match/no match task instead of testing participants on the grammatical correctness of syntactic stimuli. If participants are not explicitly pushed to interpret an incorrect prime-target pair as *grammatically* incorrect, they may just consider it as more difficult to process, and not in terms of a syntactic violation. This may prevent from generating a P600 effect. In the masked condition, we did not find any ERP effect. This may mean that feedback processing is required for syntactic unification to occur. However, we could not be sure that impairment of unification could be directly attributed to feedback disruption, since we did not find any effect in the semantic condition either.

We hypothesized that the null result in the semantic masked condition could be due to two main factors. First, we employed different lists of words for primes and targets. It has been argued that masked priming may only occur (or at least is strongly increased) when words appear as both primes and targets, thus suppressing prime novelty (Abrams & Greenwald, 2000; Damian, 2001; Van den Bussche, Van den Noortgate, et al., 2009). According to this view, when primes are also presented as targets, automatic associations between words are established, which do not need to be mediated by a semantic analysis. Second, the match/no match task required participants to judge both words within the pair. On the contrary, in tasks more commonly employed in semantic priming paradigms (e.g. lexical decision tasks, valence or animacy categorization[18]), participants only needed to judge the target word. It may be that these changes in the semantic priming paradigm increase masked semantic processing.

In order to clarify these issues, we here report a follow-up EEG experiment. In the syntactic condition, we kept the same lexical material and experimental parameters as for the previous experiment but the crucial factor is that we changed the task. This time, we required participants to judge the grammatical correctness of syntactic combinations by modifying task instructions. In the semantic condition, we implemented two main changes. First, we employed lists of animate/inanimate words, with each word appearing both as prime and target, and therefore suppressing prime novelty and inducing automatic stimulus-response

---

[18] See the meta-analysis by Van den Bussche et al. (2009) for an overview (Van den Bussche, Van den Noortgate, et al., 2009).

mappings. Second, participants were required to perform an animacy categorization task (animate/inanimate) on the target only.

We formulated two main predictions. In the unmasked condition, we expected to find typical N400 and P600 effects for semantic and syntactic stimuli, respectively. In the masked condition, we also expected an ERP effect in the semantic case, most likely an N400 effect (Deacon et al., 2000; Kiefer, 2002; Kiefer & Brendel, 2006; Kiefer & Spitzer, 2000; Mongelli et al., 2019). In the syntactic case, finding an ERP effect[19] would mean that syntactic unification does not need feedback to occur. On the contrary, a null result would replicate our previous findings and confirm that feedback processing is indeed required for unification, both semantic and syntactic, but not for lexical retrieval.

5.2. Material and Methods

5.2.1. Participants

44 subjects (28 females) participated in this study. One subject admitted not having understood the task after the EEG recording, hence was excluded from the analyses before data analysis. Data of two subjects were recorded using the wrong cap layout, hence they were also excluded from the analyses. All 41 included subjects were right-handed native Dutch speakers, aged between 18 and 35, had normal or corrected-to-normal vision, no neurological history and were naive to the purpose of the experiment. Subjects gave written informed consent prior to participation, according to the Declaration of Helsinki. They received 22 euros for their participation.

5.2.2. Stimuli

As in the previous experiment (cf. Chapter 4), in the syntactic trials we employed subject/verb pairs (e.g. *he drives*, in Dutch *hij rijdt*; see **Table 2** for a complete list of the verbs) and numeral/noun pairs (e.g. *one hat*, in Dutch *een muts*; see **Table 2** for a complete list of the nouns), forming syntactically correct or incorrect combinations (e.g. *he drives* or *one hat* vs. **he drive* or **one hats*, in Dutch *hij rijdt* or *een muts* vs. **hij rijden* or **een mutsen*). We will refer to these combinations as “syntactic-verb” and “syntactic-noun”, respectively. In the syntactic-verb pairs, the subject was either the singular third-person pronoun *he* (in Dutch *hij*) or the plural first-person pronoun *we* (in Dutch *wij*). There were 28 verbs in

---

[19] For example the early left anterior negativity/left anterior negativity (ELAN/LAN, depending of its latency of occurrence), which has been previously found in response to syntactic violations under reduced levels of awareness (Batterink & Neville, 2013; Jiménez-Ortega et al., 2014).

total. In the syntactic-noun pairs, the numeral was either *one* (in Dutch *een*) or *two* (in Dutch *twee*). There were 28 nouns in total.

In the semantic trials, we employed animate and inanimate nouns, which formed congruent or incongruent prime-target pairs (e.g. *sheep-chef* vs. *sheep-spoon*, in Dutch *schaap-chef* vs. *schaap-lepel;* see **Table 1** for a complete list of the nouns). Animate-animate and inanimate-inanimate pairs were considered as congruent, whereas animate-inanimate and inanimate-animate pairs were considered as incongruent. The lexical material included 28 nouns (14 animate and 14 inanimate). Importantly, and contrary to the previous experiment (cf. Chapter 4), all words appeared both as primes and targets. As in the previous experiment, all words appeared as both masked and unmasked primes.

All nouns and verbs were 3-8 letters long, and matched for length and frequency within stimulus type (i.e. within semantic and syntactic trials) and across stimulus type (i.e. semantic vs. syntactic trials). Frequencies were extracted from SUBTLEX-NL, a database of Dutch word frequencies based on film and television subtitles (Keuleers et al., 2010)[20]. In all conditions, the two words were presented sequentially, i.e. one after the other.

The masks consisted of ten randomly chosen uppercase letters, which were slightly overlapping to increase the density of the mask. The space between the center of each letter was 10 pixels. Words and masks were presented in Arial lowercase font with a size of 20. Stimuli were presented in white against a black background. Participants were seated at a distance of approximately 110 cm from the computer screen.

5.2.3. Experimental design

The experiment was programmed using Presentation software (Neurobehavioral Systems, Albany, NY, USA). We employed a 2 (masking strength: masked or unmasked) x 2 (target congruency: congruent or incongruent) factorial design, separating syntactic and semantic stimuli. Note that the term “target congruency” includes both syntactic correctness (syntactic trials) and semantic congruency (semantic trials). In both syntactic and semantic blocks, each block included 112 trials and lasted approximately 5 minutes. In total, there were 448 trials in the semantic trials and 896 trials in the syntactic trials, equally divided across syntactic-verb and syntactic-noun trials. Each block included 50% masked and 50% unmasked trials, randomly mixed within blocks.

---

[20] For further details about the measure employed to calculate word frequencies, as well as for statistical comparisons of length and frequency, cf. Table 1 and 2.

In masked trials, we presented a fixation cross (300 ms), a blank screen (200 ms), a first mask (67 ms), a prime (33 ms), a second mask (67 ms), a target (500 ms) and a fixation cross (700 ms). After the fixation cross, an answer screen with the options *correct/not correct* (for the syntactic trials, in Dutch *correct/niet correct*) or *animate/not animate* (for the semantic trials, in Dutch *levend/niet levend*) appeared (see **Figure 5.1A** and **5.1C** for examples of the trial structure). The position of the correct or animate answer (left or right) was randomized. In unmasked trials, we presented a fixation cross (300 ms), a blank screen (200 ms), a first blank (67 ms), a prime (33 ms), a second blank (67 ms), a target (500 ms) and a fixation cross (700 ms). Trials had a duration of 1867 ms.

Participants were instructed to respond to the target only after the answer screen appeared. The main change between this experiment and the previous study, described in Chapter 4, is that we modified task instructions. In the previous experiment, in both the syntactic and the semantic condition, participants were required to indicate whether the target matched or did not match with the prime (match/no match task). In this experiment, they were asked to indicate whether the prime-target combination was grammatically correct or incorrect (in the syntactic condition) or whether the target was animate or inanimate (in the semantic condition) by pressing either a left or a right key on the keyboard with their left or right hand, respectively. In syntactic trials, in order to make the task meaningful in the masked condition, participants were told that each block included “easy” and “difficult” trials. In the difficult trials, words were “hidden”, which made them very hard to be read. However, they had to try their best to respond correctly. Therefore, at least in the syntactic condition participants were aware that words were present in the masked condition, but they were not able to perceive them clearly. Note that in the syntactic condition participants needed to discriminate both words in order to perform the correct/incorrect task accurately. Therefore, in this case the main task allows to assess the visibility of the prime. In order to assess prime visibility in the semantic condition, we added a visibility check block at the end of the main task. Here, participants were asked to perform the animate/inanimate judgement on the masked/unmasked prime in semantic trials, as they previously did for the target.

There was no speed stress on the response. Each block included 50% congruent and 50% incongruent trials, randomly mixed within blocks. The interval between trials varied between 750 and 1250 ms, drawn from a random distribution. At the end of each block, feedback was provided on participants’ accuracy, for both masked and unmasked trials.

5.2.4. Procedure

The experiment consisted of one main EEG session. Before starting the EEG recording, participants were introduced to both task and stimuli and performed three short practice blocks of 28 trials each (one syntactic-verb, one syntactic-noun and one semantic block). Next, participants performed the main task (12 blocks: 4 syntactic-verb, 4 syntactic-noun and 4 semantic) and EEG was recorded. Block order, both in the practice and in the main task, was randomized across participants.

5.2.5. Electroencephalographic measurements

The electroencephalogram was recorded continuously from 61 active Ag/AgCL electrodes using an actiCap system (Brain Products GmbH). 59 of these electrodes were mounted on a cap with equidistant electrode montage. Two separate electrodes were placed on the left and right mastoid, respectively. Blinks were monitored through a separate electrode placed below the left eye and the closest frontal electrodes to the left eye. Horizontal eye movements were monitored through two electrodes placed on the lateral canthi next to the left and right eye. The ground electrode was placed on the forehead. EEG and EOG recordings were amplified through BrainAmp DC amplifiers. The EEG signal was recorded with a sampling rate of 500 Hz, then filtered offline with a high-pass filter of 0.1 Hz and a low-pass filter of 40 Hz. All electrode sites were re-referenced offline to the average of left and right mastoids and epoched from -0.667 (i.e. the beginning of a trial) to +1.6 s surrounding each trial. All ERPs were time-locked to target presentation. Next, trials were visually inspected and those containing artefacts not related to blinks were manually removed. Note that visual inspection was blind to the conditions of the experiment. Deleted channels were reconstructed based on a nearest neighbor approach. Independent component analysis (ICA) was computed and components containing blink/oculomotor artefacts were removed from the data. The pre-target interval between 367 and 167 ms before target (i.e. the duration of the blank before the first mask) was employed as a baseline. For follow-up analyses, we also applied a baseline correction of 200-400 ms after target onset.

5.2.6. Statistical analyses

Behavioral analyses (repeated measures ANOVAs and paired t-tests) were performed in MATLAB. For our ERP analyses, all preprocessing steps were conducted with Fieldtrip (Oostenveld et al., 2011). ERP statistical analyses were performed using a combination of Fieldtrip and MATLAB (The Mathworks, Natick, MA, USA) scripts. The ERP analysis procedure, which is the same employed for our previous experiments, is reported below. Our hypotheses focused on the N400 and P600 effects, as typical neural markers of semantic and syntactic processing, respectively[21].

As a first step, we performed cluster-based permutation tests (Maris & Oostenveld, 2007) on the time window from 0 (that is target, i.e. second word onset) to 1.2 s (i.e. the end of a trial; the answer screen was presented 1.2 seconds after the onset of the target), in order to isolate significant ERP effects related to syntactic violation or semantic incongruency (contrast incongruent vs. congruent, computed separately for syntactic and semantic stimuli). A minimum of two neighboring electrodes had to pass the threshold of $p<0.05$ to form a cluster. Cluster-based procedure was based on 10000 iterations. This Monte-Carlo method generated a nonparametric estimate of the p-value representing the statistical significance of the originally identified cluster. This analysis isolated significant effects as clusters in time and space. To visualize the evolution of significant clusters, we divided the time period (0-1.2 s) in 12 equal bins of 100 ms and plotted for each bin (i.e. 0-100, 100-200, etc.) all electrodes that were significant at least 50% of the time window (as an example, cf. **Figure 5.2A**).

Subsequently, for follow-up analyses we isolated the exact time window and channels where the effects were strongest. To do so, the onset and offset of a cluster were defined as the time period around the maximum difference where the difference did not drop below 50% of this maximum and where at least one channel showed a significant effect. We then selected the 10 channels within the cluster that showed the largest effect in this time window (for a similar procedure, cf. Mongelli et al., 2019 and Meijs et al., 2018). The resulting regions of interest (ROI) and time windows were used for subsequent analyses, including all the relevant factors. We also performed post-hoc, exploratory analyses on the N400 time window, defined based on previous literature (Kutas & Federmeier, 2010) or on ERP visual inspection, and selecting the ROIs that were defined through the cluster-based procedure. Moreover, as a control, we performed supplementary analyses on central and posterior ROIs, defined based on previous literature on the N400 (Kutas & Federmeier, 2010) and the P600 (Gouvea et al., 2010), respectively. These control analyses led to the same results.

---

[21] For a more detailed description of typical N400 and P600 effects (in terms of time window and topography), cf. the Methods section of Chapter 4.

5.3. Results

In this experiment, we aimed to shed light on some aspects of the previous experiment (cf. Chapter 4), with the main goal of clarifying whether syntactic unification requires neural feedback between distant brain areas. In particular, we investigated task-related effects on the processing of syntactic violations and semantic incongruencies.

5.3.1. Behavior

Since task differed across syntactic and semantic stimuli, we analyzed behavioral performance separately for the two types of stimuli. For syntactic stimuli, participants were asked to indicate whether the prime-target combination that was just presented was grammatically correct or incorrect, hence their answer depended on the identity of both the masked/unmasked prime and the unmasked target (the target was always fully visible). Therefore, in this case, we investigated how masking strength of the prime affected participants' accuracy. We found that masked and unmasked conditions differed significantly, with accuracy being significantly lower when primes were masked than unmasked (t_{40}=80.30, p<0.001. **Figure 5.1B**). In the unmasked condition, subjects performed well above chance (t_{40}=76.02, p<0.001, 95% correct. **Figure 5.1B**). In the masked condition, performance was much poorer and numerically close to chance level, although statistically above chance level (t_{40}=3.05, p=0.004, 51.24% correct. **Figure 5.1B**). Note that participants' accuracy did not differ across syntactic-verb and syntactic-noun trials (interaction masking strength x stimulus type: $F_{1,40}$=0.41, p=0.525).

In the semantic condition, participants were asked to indicate whether the target was animate or inanimate, therefore their answer depended on the target only (always fully visible). Therefore, in this case we tested how well they performed on the animacy categorization task. As expected, masked and unmasked conditions did not differ significantly (t_{40}=-0.84, p=0.40. **Figure 5.1D**), with accuracy being high and above chance in both conditions (unmasked: t_{40}=83.40, p<0.001, 97% correct; masked: t_{40}=135.05, p<0.001, 97% correct. **Figure 5.1D**).

During the visibility check, ran after the main EEG task, participants were required to indicate whether the masked/unmasked prime, instead of the target, was animate or inanimate. Therefore, subjects were tested on prime visibility in the semantic prime condition (irrespective of the relation to the target word). In this case, masked and unmasked conditions differed significantly, with accuracy being significantly lower in the masked condition than in the unmasked condition (t_{40}=33.87, p<0.001). In the unmasked condition, subjects performed well above chance (t_{40}=77.20, p<0.001, 96% correct), whereas in the masked condition, performance was poorer but also above chance (t_{40}=4.06, p<0.001, 54% correct).

Overall, the behavioral results showed that participants performed well in both the syntactic and semantic tasks, as revealed by high accuracy in unmasked syntactic trials and unmasked/masked semantic trials. Moreover, when subjects' response depended on both prime and target (i.e. in syntactic blocks and visibility check blocks) masking strongly affected subjects' performance, as revealed by much lower accuracy in the masked compared to the unmasked condition. However, in both masked syntactic trials and masked visibility check trials, accuracy was above chance level (51% and 54% respectively). As in the previous experiments, we cannot be sure that participants were truly unaware of the masked primes. Therefore, we do not assume that masked stimuli are fully unconscious[22].

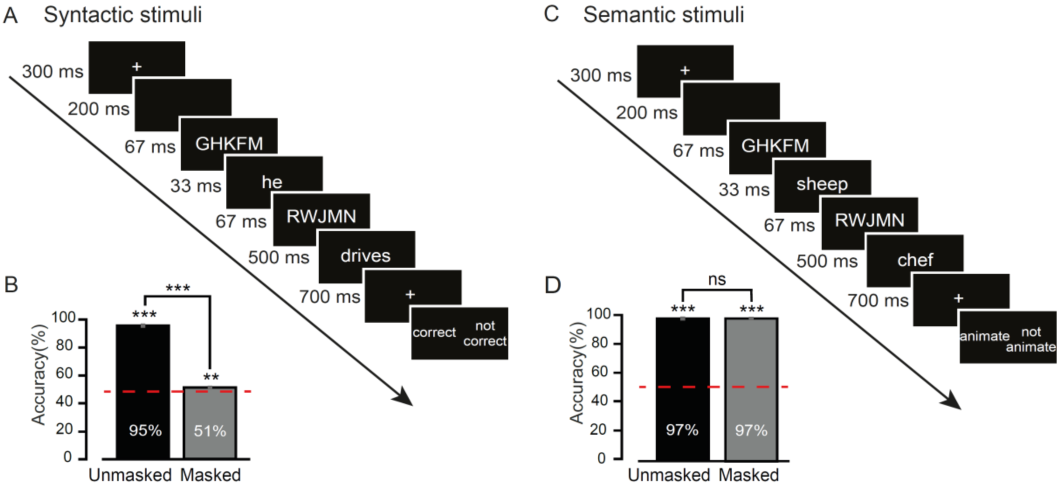

Figure 5.1: Paradigm and behavioral results. (A) Trial structure for masked syntactic stimuli. One prime (e.g. *he* or *one*) was followed by an unmasked target (e.g. *drives* or *hat*), forming syntactically correct or incorrect combinations (*he drives* vs. **he drive* or *one hat* vs. **one hats*). In the figure, a syntactically correct trial is represented. Participants were required to indicate whether prime and target formed grammatically correct or incorrect combinations. **(B)** Participants' accuracy for unmasked (black) and masked (grey) syntactic trials separately. Error bars represent between-subject SEM. **(C)** Trial structure for masked semantic stimuli. Animate nouns (e.g. *sheep* or *chef*) and inanimate nouns (e.g. *spoon*) formed congruent or incongruent prime-target pairs (e.g. *sheep-chef* vs. *sheep-spoon*). Partic-

---

[22] For a more elaborate discussion of this point, cf. the Discussion (section 3.4.3) of Chapter 3.

ipants were required to indicate whether the target was an animate or inanimate word. In the figure a congruent trial is represented. **(D)** Participants' accuracy for unmasked (black) and masked (grey) semantic trials separately. Error bars represent between-subject SEM.

5.3.2. ERP analyses

In this experiment, following up on the previous experiment (cf. Chapter 4), we explored whether a reduction of awareness through visual masking may affect syntactic unification and lexical retrieval processes. In particular, we investigated task-related effects on the processing of syntactic violations and semantic incongruencies. To this aim, in the ERP analyses we contrasted incongruent and congruent trials using cluster-based permutation testing, correcting for multiple comparisons across both time (0-1.2 s) and (electrode) space (see **Figure 5.2A** and Methods section) (Maris & Oostenveld, 2007).

First, we will report the analyses for syntactic stimuli. When isolating significant effects (incongruent-congruent) as clusters in time and space, we found a significant positive cluster over centro-frontal electrodes from 610-884 ms after target onset and peaking at 684 ms (see **Figure 5.2A**; p-value of the cluster between 610-884 ms: $p<0.001$). Next, we investigated how this ERP effect, which resembled a typical P600 effect, was modulated by masking strength. Therefore, we performed a repeated measures ANOVAs on the ERP time window found with the cluster-based permutation procedure, with two factors: masking strength (masked/unmasked), and prime/target congruency (congruent/incongruent). We found that the P600 effect was larger for unmasked than for masked trials (interaction masking strength x congruency: $F_{1,40}=15.91$, $p<0.001$). There was no difference between syntactic-verb and syntactic-noun trials, as the 3-way interaction between masking strength, congruency and stimulus type (syntactic-verb or syntactic-noun) was not significant ($p=0.437$). In post-hoc analyses, we tested the ERP effects for masked and unmasked trials separately. For unmasked syntactic stimuli, incongruent trials triggered a larger P600 compared to congruent trials ($t_{40}=-5.50$, $p<0.001$. **Figure 5.2B**), but this was not the case for masked syntactic stimuli ($p=0.116$. **Figure 5.2C**).

After visual inspection of the masked/unmasked ERPs for syntactic stimuli, we noticed a negative difference between incongruent and congruent trials in the N400 time window (**Figure 5.2B**). Therefore, in an exploratory manner, we tested this ERP difference for the centro-frontal ROI defined with the cluster-based procedure (see also inset **Figure 5.2**), and on a time window of 250-550 ms defined based on previous literature on the N400 (see dark gray highlighted area in **Figure**

5.2B and **5.2C**) (Kutas & Federmeier, 2010; Lau et al., 2008). This post-hoc analysis confirmed that there was an N400 effect in the unmasked condition (t_{40}=2.19, p=0.033. **Figure 5.2B**), but not in the masked condition (p=0.268. **Figure 5.2C**).

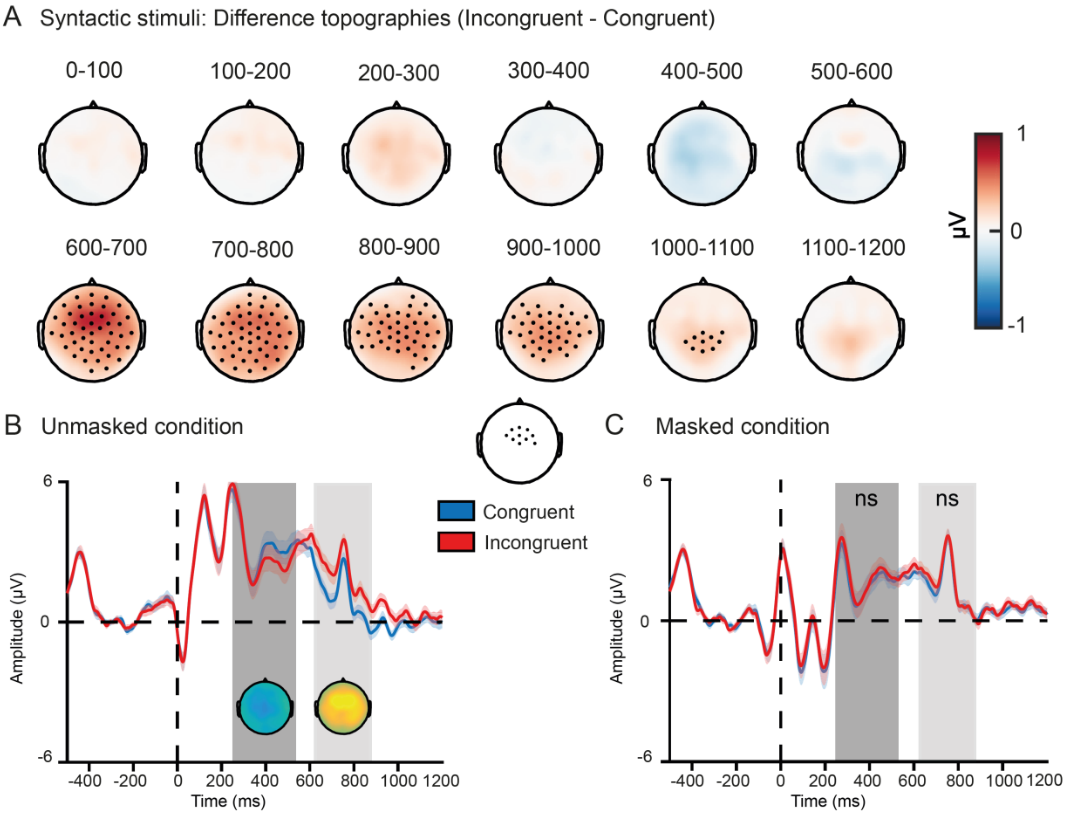

Figure 5.2: ERP effects for syntactic stimuli. (A) Topographic maps of the difference between syntactic incongruent and congruent trials over time (0 = target onset). Cluster-based permutation tests were used to isolate the significant events, while correcting for multiple comparisons across time and (electrode) space. On each head map, channels with a significant effect for at least 50% of its time window are highlighted. **(B)** ERPs for a centro-frontal region of interest (see inset) for congruent (blue) and incongruent (red) unmasked syntactic trials. **(C)** ERPs for a centro-frontal region of interest (see inset) for congruent (blue) and incongruent (red) masked syntactic trials. Inset represents the channels within the cluster that showed the largest effect in the time window 610-884 ms. In figures 5.2B and 5.2C shaded blue and red areas around the wave forms indicate between-subject SEM. Time 0 represents target onset. Shaded light grey areas highlight the time window of interest for the P600 effect (610-884 ms). Shaded dark grey areas highlight the

time window of interest for the N400 effect (250-550 ms), tested in an exploratory manner after visual inspection of the ERPs. All headmaps are scaled from -1 to 1 microvolts.

Next, we focused on the semantic stimuli. When performing the cluster-based analysis, we found a positive difference, which was significant over centro-parietal and central electrodes in the time windows 214-280 ms (peak: 248 ms) and 364-452 ms (peak: 420 ms), respectively (see **Figure 5.3A**; p-value of the cluster between 214-280 ms: p=0.003; p-value of the cluster between 364-452 ms: p=0.001). Again, we proceeded with a repeated measures ANOVA on the ERP time windows found with the cluster-based permutation procedure with the factors masking strength (masked/unmasked) and prime/target congruency (congruent/incongruent). We found that the first positivity (main effect of congruency: $F_{1,40}=33.82$, $p<0.001$) was larger for unmasked than masked trials (interaction masking strength x congruency: $F_{1,40}=12.26$, $p=0.001$). On the contrary, the second positivity was not larger for unmasked than masked trials (interaction masking strength x congruency: $F_{1,40}=0.32$, $p=0.573$). In planned post-hoc analyses, we tested the ERP effects for masked and unmasked semantic trials in both time windows separately (i.e. 214-280 ms and 364-452 ms). For the first time window (214-280 ms), there was a significant difference between congruent and incongruent trials in the unmasked condition ($t_{40}=-5.83$, $p<0.001$), but not in the masked condition ($p=0.566$). On the contrary, in the second time window (364-452 ms), there was a significant difference between congruent and incongruent trials, both in the unmasked and in the masked condition (unmasked: $t_{40}=-3.95$, $p<0.001$; masked: $t_{40}=-3.59$, $p<0.001$).

The absence of an N400 effect in the semantic stimuli was surprising and contradictory with previous studies employing similar paradigms (Holcomb, Reder, Misra, & Grainger, 2005; Kiefer & Martens, 2010). We reasoned that the N400 may be disguised because there were two neural generators active closely in time, and therefore the N400 could be overshadowed by the P200. In order to test this post-hoc hypothesis, we baseline corrected the ERPs from 200-400 ms after target onset, thereby artificially nulling the P200 effect to test whether there was a residual N400 effect after doing so. Next, in an exploratory manner, we tested the difference between congruent and incongruent trials on the central ROI defined by the cluster-based procedure (corresponding to the second positive cluster, see **Figure 5.3A**) in the 400-600 ms time-window, based on visual inspection of the unmasked ERPs (Kutas & Federmeier, 2010; Lau et al., 2008). This post-hoc analysis revealed that the early P200 effect indeed masked a subsequent N400 effect in the unmasked condition (t_{40}=3.15, p=0.003. **Figure 5.4A**), but not in the masked condition (t_{40}=-2.28, p=0.028. The effect was significant, but in the opposite direction. **Figure 5.4B**).

In summary, in this experiment we found a P600 effect in unmasked syntactic stimuli. In unmasked semantic stimuli we observed a positive difference, starting around 200 ms, between incongruent and congruent trials. This positive difference may have masked a subsequent N400 effect, which became visible when applying a baseline correction of 200-400 ms after target onset (exploratory analysis). Importantly, this positivity was also present in the masked semantic condition (but only in the time window 364-452 ms).

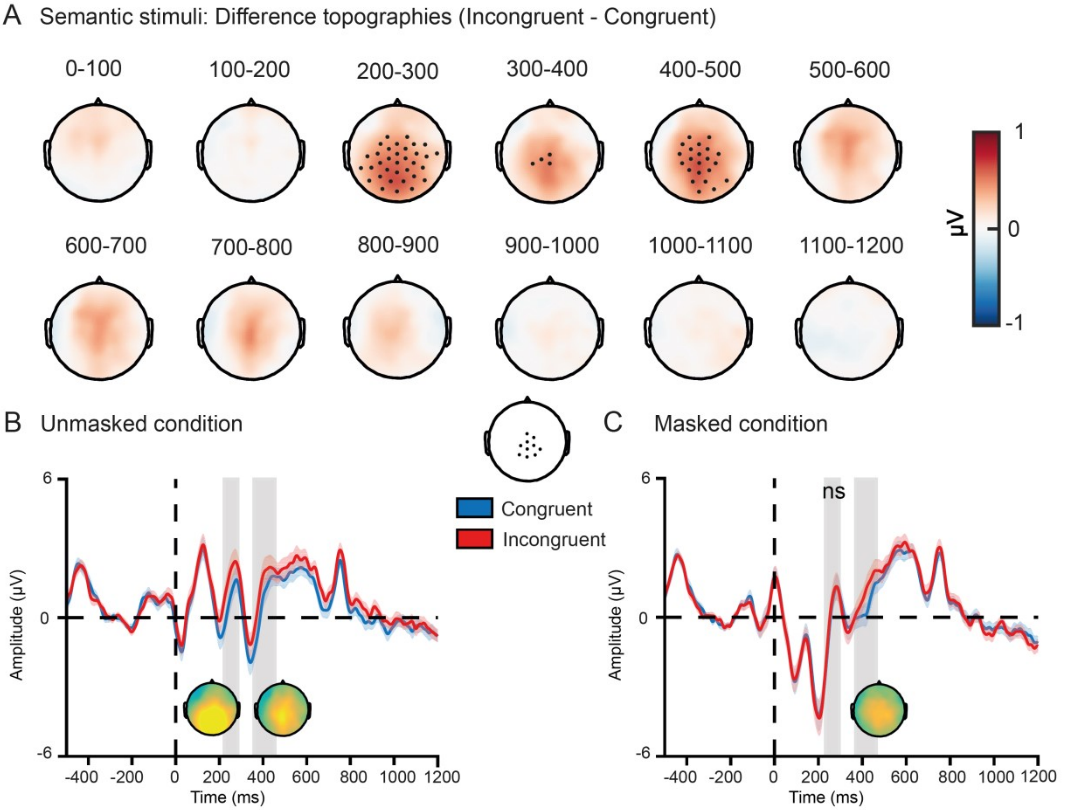

Figure 5.3: ERP effects for semantic stimuli. (A) Topographic maps of the difference between semantic incongruent and congruent trials over time (0 = target onset). Cluster-based permutation tests were used to isolate the significant events, while correcting for multiple comparisons across time and (electrode) space. On each head map, channels with a significant effect for at least 50% of its time win-

dow are highlighted. **(B)** ERPs for a central region of interest (see inset) for congruent (blue) and incongruent (red) unmasked semantic trials. Note that the early positive effect shown in the headmap (214-280 ms) was tested on a different, centro-parietal region of interest obtained with the cluster-based permutation procedure (see Results). **(C)** ERPs for a central region of interest for congruent (blue) and incongruent (red) masked semantic trials. Inset represents the channels within the second positive cluster that showed the largest effect in the time window 364-452 ms. In both figures 5.3B and 5.3C shaded blue and red areas around the wave form indicate between-subject SEM. Time 0 represents target onset. Shaded grey areas highlight the time window of interest for the two positive effects (214-280 ms and 364-452 ms). All headmaps are scaled from -1 to 1 microvolts.

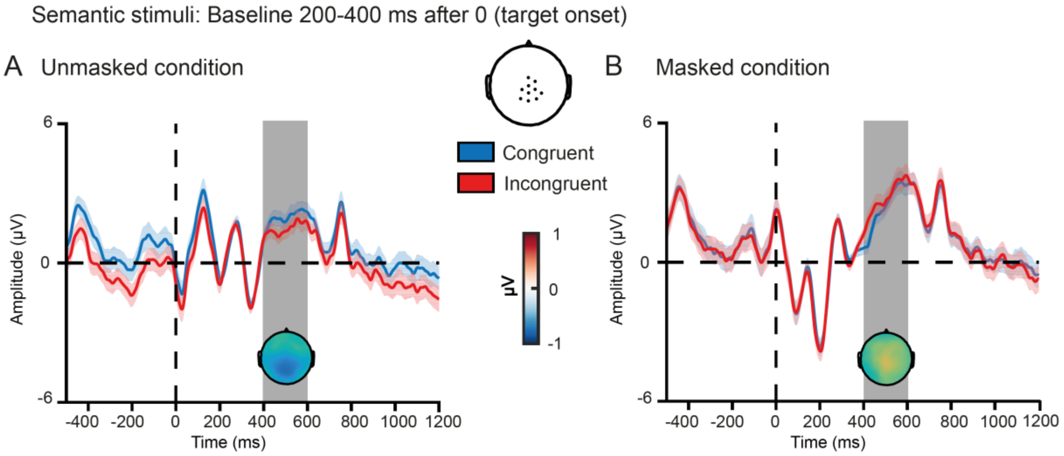

Figure 5.4: ERP effects for semantic stimuli with baseline correction of 200-400 ms after 0 (target onset). (A) ERPs for a central region of interest (see inset) for congruent (blue) and incongruent (red) unmasked semantic trials. **(B)** ERPs for a central region of interest for congruent (blue) and incongruent (red) masked semantic trials. Inset represents the channels within the second positive cluster (see **Figure 5.3A**) that showed the largest effect in the time window 364-452 ms. In both figures 5.4A and 5.4B shaded blue and red areas around the wave form indicate between-subject SEM. Time 0 represents target onset. Shaded grey areas highlight the time window of interest for the N400 effect (400-600 ms), tested in an exploratory manner after applying a baseline correction between 200-400 ms after target onset. All headmaps are scaled from -1 to 1 microvolts.

5.4. Discussion

In this study, we explored the role of feedback in syntactic unification compared to lexical retrieval, i.e. single word processing. According to the Memory, Unification and Control (MUC) model, feedback between the left inferior frontal cortex (LIFC) and the left posterior temporal cortex (LPTC) is crucial for unification, both at the semantic and the syntactic level (Hagoort, 2005, 2013, 2017; Hultén et al., 2019; Snijders et al., 2009). In previous work, we investigated this topic and found that long-range feedback, potentially involving LIFC, is required for semantic unification (Mongelli et al., 2019). Semantic and syntactic unification are thought to rely on partially different regions within the LIFC, with ventral and dorsal areas that subserve semantic and syntactic unification, respectively (Hagoort & Indefrey, 2014). Therefore, semantic and syntactic unification may also rely on different brain mechanisms and should, therefore, be tested separately. For this reason, we ran a new experiment in order to investigate syntactic unification. Following the same reasoning, we disrupted long-range feedback through visual masking and explored whether, under these conditions, syntactic unification mechanisms were spared.

In a first experiment, described in Chapter 4, we measured ERPs in response to syntactically correct/incorrect combinations (e.g. *he drives* vs. **he drive*), and semantically congruent/incongruent word pairs (e.g. *winter-summer* vs. *winter-core*). In both syntactic and semantic pairs, the first word could be either fully visible or masked from awareness. In the unmasked condition, we found an N400 effect for both syntactic and semantic stimuli. In the case of syntactic stimuli, this was against our predictions as we expected incorrect combinations to trigger a P600 effect, i.e. a typical neural marker of syntactic violation (Hagoort et al., 1993; Osterhaut & Holcomb, 1992). As a post-hoc explanation, we reasoned that this could be a task-related effect, since participants were not tested on the grammatical correctness of prime/target pairs, but on a generic match/no match task. If task instructions do not explicitly require to consider an incorrect prime-target combination as *grammatically* incorrect, participants may just interpret it as "more difficult" to process, and not in terms of a violation of syntactic constraints. This may generate an N400 effect instead of a P600 effect. In the masked condition no ERP effect was found, neither for syntactic trials nor for semantic trials. We hypothesized that the null result in the single word condition may be attributed to prime novelty and/or task-related effects. First, it has been argued that prime novelty reduces masked priming effects, as it impedes the formation of automatic, non-semantic stimulus-response associations, in favor of purely semantic associations (Abrams & Greenwald, 2000; Damian, 2001; Van den Bussche, Van den Noortgate, et al., 2009). Second, the match/no match task required participants to judge both prime and target, while in more common masked priming tasks (e.g. lexical decision tasks, valence or animacy categorization[23]), participants were required to judge the target word only.

In a follow-up experiment, we aimed to clarify these issues. We ran a new EEG experiment while implementing three main changes in the previous paradigm: (i) we changed the instructions in such a way that in the syntactic condition, participants were explicitly required to judge the grammatical correctness of the combinations; (ii) in the semantic condition, words occurred both as prime and as target; (iii) in the semantic condition, participants performed an animacy categorization task (animate/inanimate judgement) on the target word only.

In the syntactic condition, in which participants performed the task based on both prime and target, behavioral performance was very similar to the previous experiments, being higher in the unmasked than in the masked condition and therefore showing that masking significantly reduced prime visibility. In the semantic condition, in which the task only required to judge the target, the paradigm worked as predicted as participants performed well and very similarly in the masked and unmasked conditions. In EEG, in the unmasked syntactic condition we found a strong P600 effect, confirming that task settings may modulate ERP signatures of syntactic processing. In the unmasked semantic condition, we observed a positivity (starting around 200 ms) that may have masked a subsequent N400 effect. This N400 effect seemed present, although delayed, when we applied a baseline correction between 200-400 ms, thereby masking the P200 effect. The later positive effect (364-452 ms) was also present in the masked semantic condition, confirming that prime novelty and/or task may affect masked semantic processing. In the masked syntactic condition, no ERP effect was found. On this last point, the current study replicates the previous experiment (cf. Chapter 4), in which no effect of syntactic unification under reduced levels of awareness was found. Taken together, the two experiments suggest that awareness is crucial for syntactic unification, and therefore long-range feedback processing, potentially implying frontal areas, may be required for syntactic unification, but not for lexical retrieval.

5.4.1. The role of awareness in syntactic unification

Our findings suggest that awareness plays an important role in syntactic combinatorial processes. As previously noticed, there are only a few studies investigat-

---

[23] See the meta-analysis by Van den Bussche et al. (2009) for an overview (Van den Bussche, Van den Noortgate, et al., 2009).

ing syntactic processing under reduced levels of awareness, and results are mixed. Our findings are consistent with previous work, in which no evidence for syntactic unification under reduced awareness was found (Batterink et al., 2010), and in contrast with other studies suggesting that syntactic unification under reduced awareness may be possible (Batterink & Neville, 2013; Berkovitch & Dehaene, 2019; Hung & Hsieh, 2015; Jiménez-Ortega et al., 2017, 2014; Pulvermüller & Shtyrov, 2003).

However, we argue that some effects in these previous studies (Batterink & Neville, 2013; Pulvermüller & Shtyrov, 2003) may be explained by other factors than syntactic unification processes. Batterink & Neville (2013) used a cross-modal attentional blink (AB) paradigm to investigate undetected syntactic violations within sentences. They presented a tone (first target) either immediately before or after the onset of a visually presented syntactic violation (e.g. **We drank Lisa's by brandy the fire in the lobby*) (second target). Sometimes participants missed these syntactic violations, because the tone attracted their attention and prevented the violation from reaching awareness (attention blinked). Interestingly, using EEG, they found that both detected and undetected syntactic violations triggered an early left negative response (ELAN), whereas only detected violations triggered a P600 effect. Nevertheless, it has been shown that the attentional blink impairs conscious report behaviorally, but does not disrupt perceptual integration mechanisms and may leave local feedback processing intact (Dehaene et al., 2006; Fahrenfort et al., 2017; Luck, Vogel, & Shapiro, 1996). Therefore, this leaves open the question whether syntactic unification can occur in the absence of feedback (masking does disrupt feeback). In a previous AB study, Batterink & Neville (2010) did not find any evidence of syntactic processing under reduced levels of awareness. They measured ERP responses to syntactically correct/incorrect word pairs (e.g. *the sky* vs. **we sky*) and found that ERPs to targets occurring outside the AB period triggered an N400-like negativity, while ERPs in response to unattended targets showed no ERP effect. Their previous conclusion, i.e. that full awareness is necessary for syntactic unification, is consistent with our findings. These results, which seem to be contradictory with their more recent findings, are not discussed by Batterink & Neville (2013).

The study by Pulvermüller & Shtyrov (2003) can also be explained by factors not related to unification. They investigated violations of grammatical agreement in number (*we come* vs. **we comes*), which were presented auditory while subjects' attention was distracted (they were instructed to watch a silent video and ignore the auditory stimuli). They found that grammatically incorrect sentences elicited a larger mismatch negativity (MMN)[24] effect compared to grammatically correct ones. However, as argued above, attentional deviation is not thought to disrupt feedback. Moreover, the latency of the MMN (348 ms) is a typical N400 latency, hence it is not clear why they consider it as an MMN. Last, they only employed one sentence (i.e. *we come* vs. **we comes*), which was repeated throughout the whole experiment. Their findings should be replicated with a larger stimulus set before inferring general conclusions.

Other studies (Berkovitch & Dehaene, 2019; Hung & Hsieh, 2015; Iijima & Sakai, 2014; Jiménez-Ortega et al., 2017, 2014) may have methodological issues explaining the observed syntactic unification effects. For example, Berkovitch & Dehaene (2019) investigated masked syntactic priming in a series of behavioral experiments[25]. In one of these experiments, they investigated correct/incorrect word combinations (for example determiner-noun vs. pronoun-noun combinations, e.g. *the sport* vs. **he sport*, or determiner-verb vs. pronoun-verb combinations, e.g. **the sleeps* vs. *he sleeps*). They found that masked incorrect combinations resulted in longer reaction times (RTs) to the target, compared to correct combinations (although the effect was small: 7 ms, p=0.032, one-tailed). However, the effect seemed only present for verb targets (i.e. determiner-verb vs. pronoun-verb) and absent for masked noun targets, which leaves open the generalizability of the observations. Further, as the authors themselves acknowledge, the priming effect may have been driven by differences in transitional probabilities between conditions, that is by the fact that correct combinations are more frequent than incorrect combinations in natural language. It has been shown that transitional probabilities between words affect language processing, both at the behavioral (Thompson & Newport, 2007) and the neural level (Kutas & Hillyard, 1984). In two follow-up experiments, the authors controlled for this factor, and while doing so, they failed to replicate the initially observed priming effect.

Ortega et al. (2014) investigated gender agreement violations. They presented masked/unmasked adjectives, which could be either syntactically correct or incorrect with respect to a visible sentence context (e.g. *El detective privado investiga* vs. **El detective privada investiga*. In English: *The private*$_{[mas.]}$ *detective*$_{[mas.]}$ *investigates* vs. **The private*$_{[fem.]}$ *detective*$_{[mas.]}$ *investigates*). EEG revealed that masked incorrect noun-adjective pairs triggered an ELAN, followed by a P600-like modulation, whereas unmasked incorrect noun-adjective pairs only triggered a

---

[24] The MMN is a negative ERP effect triggered by the presentation of a deviant event, embedded in a stream of repeated and familiar events (Garrido, Kilner, Stephan, & Friston, 2009).

[25] Here we only discuss the experiments investigating syntactic priming at the unification level. In the other experiments, they investigated masked syntactic priming at the single word level (e.g. priming of a noun target by another noun vs. by a verb).

P600[26]. However, in this paradigm the correct/incorrect adjective was presented twice (first masked, then unmasked), hence the results may stem from repetition suppression, and not gender agreement violations.

Ortega et al. (2017) employed a similar paradigm, but in this case the masked adjective was neutral, positive or negative. They found again ERP effects triggered by the masked adjectives, differentially modulated for neutral, positive and negative adjectives (a LAN+P600, early P600 and N400 effects for neutral, negative and positive adjectives, respectively). However, they excluded 1/3 of the subjects for admitting stimulus awareness. Post-hoc exclusion of subjects based on awareness measures has raised methodological criticisms for issues related to the regression to the mean (Shanks, 2017).

Hung & Hsieh (2015) investigated syntactic incongruency with continuous flash suppression (CFS). They presented visible Subject-Verb combinations (e.g. *Birds eat*), followed by a syntactically congruent (Object, e.g. *worms*) or incongruent (Verb, e.g. *drank*) word. This last word was masked with CFS. They found that the third word in the syntactically incongruent condition broke suppression faster than the word in the congruent condition. However, similarly to Berkovitch & Dehaene (2019), their results may be explained by differences in transitional probabilities between the correct and incorrect condition. Moreover, CFS has been recently criticized, especially when breakthrough times are used as dependent measure, and it is currently controversial whether CFS can be considered as an accurate method to study information processing during unawareness or whether these effects may be driven by post-breakthrough processes (Stein, Hebart, & Sterzer, 2011).

Iijima & Sakai (2014) performed a magnetoencephalography (MEG) study comparing syntactically correct and incorrect combinations in Japanese. For example, in one type of combinations an unmasked object was followed by a transitive/intransitive masked verb and a target verb. The masked verb thus affected the grammaticality of the sentence, forming congruent (object - transitive verb prime - target verb) or incongruent (object – intransitive verb prime – target verb) combinations. They found that some congruent combinations triggered an increased response in LIFG, interpreted as a marker of reinforcement of prior expectations. However, this effect was not found in all correct/incorrect combination types. Therefore, similarly to the results by Berkovitch & Dehaene (2019), one

---

[26] Note that this is in contrast with the findings by Batterink & Neville (2013), who found a suppression of the P600 effect in the awareness-reduced condition, and both an ELAN and a P600 effect in the fully conscious condition.

may wonder if their findings – although interesting – allow to formulate general conclusions about syntactic processing.

Overall, previous work on syntactic processing under reduced levels of awareness may not specifically tackle syntactic unification, or may suffer from methodological issues that first need to be explored further before conclusions can be drawn. Moreover, as previously noticed for semantic unification, studies on sentence processing under reduced levels of awareness may not fully distinguish between unification and lexical retrieval processes. To the best of our knowledge, our studies are the first that aim to control for this issue.

5.4.2. The influence of task on syntactic processing

One important goal of this study was investigating the influence of task requirements on syntactic processing. In a previous experiment (cf. Chapter 4), we found that syntactic violations (e.g. *he drives* vs. **he drive*) triggered an N400 effect, instead of the expected P600 effect. As a post-hoc explanation, we hypothesized that this could be a task-related effect, since participants were tested on a generic match/no match task between prime and target, without being explicitly required to judge the grammaticality of syntactic combinations. This may lead participants to interpret incorrect prime-target combinations as simply “more difficult” to process, instead of syntactically incorrect. Therefore, in the current experiment, we modified the task and asked participants to judge the grammatical correctness of combinations, while keeping the same lexical material. Results confirmed our predictions, as in this case syntactic violations triggered a P600 effect. A tentative explanation is provided below.

In a previous study, N400 effects triggered by syntactic violations have been found in aphasic patients. Hagoort et al. (2003) investigated syntactic processing in patients with agrammatic aphasia. These patients, due to a perisylvian lesion in the language-dominant hemisphere, usually suffer from a significant reduction of their ability to exploit syntactic constraints, i.e. rules that specify how to combine words in a grammatically well-formed manner. When tested on a word order violation task (e.g. **the thief steals the expensive very clock* vs. *the thief steals the very expensive clock*), agrammatic patients showed an N400 effect instead of a typical P600 effect, which was observed in healthy controls and non-agrammatic aphasics. Hagoort et al. argued that this N400 effect may reflect the tendency of agrammatic patients to perform sentence comprehension by employing semantic constraints (Hagoort et al., 2003). Since the syntactic route was no longer available for them, they may have tried to solve the sentence-binding problem through a substitutive semantic route[27]. Accordingly, they treated the difference between sentences with the correct word order and the sentences with the wrong word order as a difference between transitional probabilities (**the expensive very clock* is less likely to occur than *the very expensive clock*). Differences in transitional probabilities are known to modulate the N400 (Kutas & Hillyard, 1984). Therefore, sentences with the wrong word order triggered a larger N400, compared to sentences with the correct word order.

We suggest that a similar explanation may hold for our findings. In the previous experiment, participants may have been pushed to employ the semantic route instead of the syntactic route by task requirements, even if in their case both routes were intact. Task instructions did not explicitly ask to consider an incorrect prime-target combination as *grammatically* incorrect, hence participants may have interpreted it as generally "more complicated". In this case, the N400 effect may reflect a general cost of processing resources in solving a semantic binding problem, replacing the expected P600 effect. In the current experiment, the task instructions explicitly required participants to follow a syntactic route towards a correct answer, thus eliciting a typical P600 effect. However, this is a speculative explanation that should be confirmed by future studies.

Taken together, the two experiments suggest that task requirements may strongly influence semantic/syntactic processing, pushing comprehenders to employ the semantic route instead of the syntactic route to process syntactic violations, even if both routes are available. In future work, it would be interesting to test task influence on N400/P600 effects in the opposite direction, that is triggering P600 effects in semantic processing (instead of N400 effects) by modifying task requirements. That would show that semantic processing, as reflected by N400 effects, can be influenced by task requirements, similarly to what we found here for syntactic processing.

5.4.3. The influence of task on semantic processing

Our findings highlight that task settings may also play a role in semantic processing, for both masked and unmasked semantic material. In the semantic condition, we did not observe that incongruent pairs triggered an N400 effect, against our expectations. Instead, we observed an early positivity, starting at ~200 ms (which in fact may have masked the N400 effect, which became visible when masking the P200 effect by applying a different baseline correction). In the language literature, P200 effects have mostly been associated with low-level lexical

---

[27] This interpretation assumes that language processing is performed along two processing routes at least, i.e. one semantic route and one syntactic route.

processes, like phonological (Kong et al., 2010) and morphological processes (Beyersmann, Iakimova, Ziegler, & Colé, 2014). For example, Beyersmann et al. (2014) found that a P200 effect when comparing morphologically related prime-target pairs (e.g. *washing-wash*) to unrelated pairs. Semantic-related P200 is less common, but has been documented in some cases (Stuellein, Radach, Jacobs, & Hofmann, 2016). For example, Stuellein et al. (2016) compared words with many semantic associates (within the stimulus set) with words with a smaller number of semantic associates in a recognition memory task. They observed a larger P200 for words with many associates compared to few associates. In our data, the positive difference between incongruent and congruent trials in the masked condition was only present in the later time window (364-452 ms).

As already noticed, the fact that we found a positive difference between congruent and incongruent trials, both in the masked and the unmasked case, was not in line with our initial hypotheses. This unexpected result could be driven by specificities of the task settings. In our paradigm, participants had to classify the target as animate or inanimate. It has been shown that classifying a visual input (a picture) as animate or inanimate may only take 150 ms (Thorpe, Fize, & Marlot, 1996). Therefore, the positive effect may reflect the influence of the prime on this fast animacy categorization process. Moreover, since task instructions did not explicitly mention the congruency factor between prime and target, participants were not focused on it. A congruency effect (i.e. an N400 effect) was nevertheless present (even if masked by the early positivity) in the unmasked condition, where the prime was fully visible. In the masked case, the task-irrelevance of the congruency factor may explain the absence of the N400 effect. These findings add evidence to a growing body of literature showing that task relevance strongly affects masked processing (Berkovitch & Dehaene, 2019; van Gaal, de Lange, & Cohen, 2012).

We acknowledge that these results may also be explained by aspects of the lexical material we may not have fully controlled for, e.g. semantic associations between animate and inanimate stimuli. For example, *sailor* and *storm* are incongruent from the animacy perspective, thus are considered as an incongruent pair in our experimental paradigm. However, from the semantic association point of view, they may be considered as related, hence they would be considered as a congruent pair by the brain implicitly. This is a limitation of the present study, which should be better taken into account in future work. It would be useful to replicate the current experiment with a match/no match task (similar to the task that we employed in previous studies) and keeping the same lexical material.

The fact that we found a masked ERP effect in the current experiment, while no effect was present in the previous study, may be explained by two factors. First, in this study, contrary to the previous study, all words appeared both as primes and targets. As explained above, it has been shown that abolishing prime novelty enhances masked priming effects, as automatic, non-semantic associations are established between prime and target (Abrams & Greenwald, 2000; Damian, 2001; Van den Bussche, Van den Noortgate, et al., 2009). This may have triggered a difference between congruent and incongruent conditions in the present study.

Second, in this experiment participants responded based on the target only (animacy categorization task), while in the previous study they responded based on both prime and target (match/no match task). It has been shown that task settings may influence masked semantic priming effects. For example, Kiefer & Martens (2010) showed that semantic tasks (e.g. animacy categorization) trigger a larger N400 effect compared to perceptual tasks (e.g. decision on open/close shape of first and last letter) in masked semantic paradigms (Kiefer & Martens, 2010). However, to the best of our knowledge, there is no literature on differences in masked priming effects when the task requires a response on both prime and target vs. on the target only. This could also be a matter for future studies. Moreover, we cannot state which factor (prime novelty and/or task settings) was decisive in triggering an ERP effect in the current study compared to the previous study. This issue should also be investigated in follow-up experiments modifying prime novelty and task requirements separately.

5.4.4. Conclusion

This work, together with the previous study (reported in Chapter 4), suggests that full awareness is required for combining words into larger syntactic structures. Indeed, when reducing stimulus awareness with visual masking, which at the same time disrupts long-range feedback, syntactic unification is impaired, while lexical retrieval is preserved (at least under certain conditions). Our findings provide evidence in favor of the hypothesis that feedback processing, potentially implying frontal areas, is crucial for syntactic unification mechanisms (Hagoort, 2017; Hultén et al., 2019; Snijders et al., 2009; Tyler et al., 2011).

Acknowledgements

We thank Birgit Knudsen, Eva Poort and Iris Schmits for their valuable assistance with data acquisition.

5.5. Tables

Semantic stimuli			
Animate words	**Frequency - Lg10WF**	**Word length**	**Translation**
schaap	2,4579	6	sheep
egel	1,415	4	hedgehog
stier	2,6243	5	bull
paard	3,5632	5	horse
vogel	3,1498	5	bird
leeuw	2,8089	5	lion
insect	2,3304	6	insect
chef	3,1332	4	chef
dame	3,5586	4	lady
zeeman	2,3424	6	sailor
monnik	2,4166	6	monk
spion	2,9085	5	witch
agent	3,9117	5	agent
paus	2,7427	4	pope
Mean	2,811	5	
SD	0,637	0,784	
Inanimate words	**Frequency - Lg10WF**	**Word length**	**Translation**
lepel	2,3424	5	spoon
suiker	2,98	6	sugar
villa	2,5224	5	villa

storm	3,1126	5	storm
fiets	2,9786	5	bike
naald	2,5717	5	needle
kwast	1,8808	5	brush
kamer	4,0805	5	room
piano	2,791	5	piano
broek	3,4688	5	trousers
stoel	3,3502	5	chair
wijn	3,4223	4	wine
peper	2,2227	5	pepper
beugel	2,1847	6	ring
Mean	2,850	5,071	
SD	0,607	0,474	
	Animate vs. Inanimate words		
Frequency	p=0,870		
Word length	p=0,806		

Table 1. List of semantic stimuli (column 1) with relative frequency (column 2), length (column 3) and English translation (column 4). Mean and standard deviation (SD) of word frequencies and word length are reported in column 2 and 3, respectively. Animate and inanimate nouns formed congruent or incongruent prime-target pairs (e.g. *sheep-chef* vs. *sheep-spoon*, in Dutch *schaap-chef* vs. *schaap-lepel*). The lexical material included 28 nouns (14 animate and 14 inanimate). Contrary to the previous experiment (cf. Chapter 4), all words appeared both as primes and targets. As in the previous experiment, frequencies were extracted from SUBTLEX-NL, a database of Dutch word frequencies based on film and television subtitles (Keuleers et al., 2010). Our measure for frequency was Lg10WF, i.e. the logarithm to the base 10 of FREQcount+1, where FREQcount is the number of times the word

appeared in the corpus (i.e. on the total of 43.8 million words). According to Keuleers et al. (2010), calculating the log frequency on the raw frequencies is the most straightforward transformation, because it allows researchers to give words that are not in the corpus a value of 0. All words were matched for length and frequency (p-values reported in the table).

Syntactic stimuli - Verbs	**Frequency-Lg10WF**	**Word length**	**Translation**
rijden	3,817	6	drive
niezen	1,9294	6	sneeze
lezen	3,6735	5	read
zingen	3,4573	6	sing
klagen	2,937	6	complain
bijten	2,8445	6	bite
rennen	3,5047	6	run
raden	3,0917	5	guess
kopen	3,7569	5	buy
roken	3,2833	5	smoke
lopen	3,9863	5	walk
verven	2,29	6	paint
winnen	3,7074	6	win
bidden	3,2071	6	pray
rijdt	3,3294	5	drives
niest	1,4314	5	sneezes
leest	3,0465	5	reads
zingt	2,8639	5	sings
klaagt	2,4472	6	complains
bijt	2,8733	4	bites
rent	2,6893	4	runs

raadt	2,3502	5	guesses
koopt	2,9795	5	buys
rookt	2,7292	5	smokes
loopt	3,7778	5	walks
verft	1,4472	5	paints
wint	3,3212	4	wins
bidt	2,2253	4	prays
Mean	2,964	5,214	
SD	0,683	0,686	
Syntactic stimuli - Nouns	**Frequency - Lg10WF**	**Word length**	**Translation**
kast	3,1189	4	wardrobe
kruk	2,0531	4	stool
hand	3,9417	4	hand
stoel	3,3502	5	chair
trein	3,5051	5	train
muts	2,2923	4	hat
jurk	3,3872	4	dress
bank	3,6042	4	bench
kers	1,8573	4	cherry
hond	3,8678	4	dog
nicht	3,0022	5	niece
agent	3,9117	5	agent
jurist	2,1903	6	lawyer
rat	2,9978	3	rat
kasten	2,0792	6	wardrobes

krukken	1,8692	6	stools
handen	3,9729	6	hands
stoelen	2,6911	7	chairs
treinen	2,444	7	trains
mutsen	1,1761	6	hats
jurken	2,4829	6	dresses
banken	2,6222	6	benches
kersen	2,017	6	cherries
honden	3,3514	6	dogs
nichten	2,0828	7	nieces
agenten	3,4293	7	agents
juristen	1,8633	8	lawyers
ratten	2,8854	6	rats
Mean	2,787	5,392	
SD	0,772	1,257	
	Semantic stimuli vs. Syntactic stimuli (Verbs)	**Semantic stimuli vs. Syntactic stimuli (Nouns)**	**Syntactic stimuli (Verbs) vs. Syntactic stimuli (Nouns)**
Frequency	p=0,439	p=0,817	p=0,323
Word length	p=0,345	p=0,231	p=0,524

Table 2. List of syntactic stimuli (nouns and verbs, column 1), with relative frequency (column 2), length (column 3) and English translation (column 4). The lexical material is the same as in the previous experiment (cf. Chapter 4). Mean and standard deviation (SD) of word frequencies and word length are reported in column 2 and 3, respectively. As in the previous experiment, verbs were combined with the singular third-person pronoun *he* (in Dutch *hij*) or the plural first-person pronoun *we* (in Dutch *wij*), forming syntactically

correct or incorrect combinations (e.g. *he drives* vs. **he drive*, in Dutch *hij rijdt* vs. **hij rijden* or *we drive* vs. **we drives*, in Dutch *wij rijden* vs. **wij rijdt*). Nouns were combined with the numeral *one* (in Dutch *een*) or *two* (in Dutch *twee*), forming syntactically correct or incorrect combinations (e.g. *one hat* vs. **one hats*, in Dutch *een muts* vs. **een mutsen* or *two hats* vs. **two hat*, in Dutch *twee mutsen* vs. **twee muts*). Our measure for frequency was Lg10WF (see legend of Table 1 for further details). All words were matched for length and frequency (p-values reported in the table).

6

General discussion

6.1. Summary

The goal of this thesis was to investigate the neural mechanisms subserving sentence and single word processing, focusing on the role of long-range feedback in sentence processing. Sentence processing requires combining single words into larger units that are well-formed, both at the semantic and the syntactic level. Within the Memory, Unification and Control (MUC) model (Hagoort, 2005, 2013, 2017), the term unification refers to language combinatorial processes. Unification is a property of the language faculty across semantic, syntactic and phonological domains (Jackendoff, 2002, 2007). Semantic unification is defined as “the integration of word meaning into an unfolding representation of the preceding context” (Hagoort et al., 2009). Syntactic unification is defined as the combination of lexical items (words or chunks of structures, e.g. adjective+noun) retrieved from memory into larger structures (e.g. noun or verb phrases[28]). Syntax is not reducible to semantics, and *vice versa* (Adger, 2018; Chomsky, 1957). Moreover, semantic and syntactic processes are thought to rely on partially different brain mechanisms (Ferreira & Clifton, 1986; Friederici et al., 2000; Hagoort & Indefrey, 2014; Newman et al., 2003). This suggests that semantic and syntactic unification should be tested separately. Within the MUC framework, both semantic and syntactic unification rely on a large network that, crucially, involves the left inferior frontal cortex (LIFC). Feedback processing between the LIFC and the left posterior temporal cortex (LPTC) is therefore thought to be necessary for unification but not for lexical retrieval, i.e. single word processing, which is supposed to rely on processes within the LPTC (Hagoort, 2017; Hultén et al., 2019; Snijders et al., 2009).

In this work, I employed visual masking to test the MUC hypothesis that feedback processing, likely involving LIFC, is crucial for semantic and syntactic unification. Visual masking is thought to disrupt long-range feedback processing, potentially implying frontal areas, while preserving feedforward processing[29] (Del Cul et al., 2009; Fahrenfort et al., 2007, 2017). Previous research on masked processing has shown that masked single words trigger behavioral and neural markers of language processing, both at the semantic and the syntactic level[30]. On the contrary, it is more debated whether more complex semantic and syntactic information

---

[28] A noun phrase is a word or group of words that function as the subject, the object or the complement of a sentence. A noun or a pronoun is usually the headword of the phrase. A verb phrase is a word or group of words containing a verb as the headword of the phrase. The head verb is often accompanied by an auxiliary verb, complements, objects and/or modifiers.

[29] For an extensive discussion of this point, cf. the Discussion (section 3.4.2) of Chapter 3.

[30] For a review of masked semantic priming effects, cf. Kouider & Dehaene (2007) and the meta-analysis by Van den Bussche et al. (2009). For a review of masked syntactic priming effects, cf. the recent study by Berkovitch & Dehaene (2019) and the Discussion (section 5.4.1) of Chapter 5.

(multiple words or full sentences) can be treated under reduced levels of awareness (Batterink et al., 2010; Rabagliati et al., 2018).

In this thesis, in a series of four electroencephalography (EEG) experiments I employed visual masking to disrupt feedback and investigated whether, under these conditions, unification processes were spared. I focused on N400 and P600 effects, considered as typical markers of semantic and syntactic processing, respectively (Kos, Vosse, van den Brink, & Hagoort, 2010). I aimed to answer two main questions:

1. Is feedback processing necessary for semantic unification (Chapter 2 and 3)?
2. Is feedback processing necessary for syntactic unification (Chapter 4 and 5)?

Overall, I found that masking disrupts both semantic and syntactic unification processes, while preserving lexical retrieval. Across the four experiments, in both sentence and single word unmasked conditions I found clear neural signatures of semantic and syntactic processing, reflected by strong N400 and P600 effects. On the contrary, in the masked condition I only found event-related potential (ERP) effects at the single word level (and only under certain experimental conditions), but not at the sentence level. Taken together, these findings suggest that feedback processing between distant brain areas is required for unification, but not for lexical retrieval.

6.2. Implications and outlook for language models

These findings confirm a core prediction of the MUC model. The importance of long-range feedback mechanisms for sentence processing has also been highlighted by other language models (Friederici, 2002), in contrast with purely feedforward models (Cutler & Clifton, 1999). My results are consistent with previous studies investigating the temporal dynamics of sentence and single word processing (Hultén et al., 2019; Lam, Schoffelen, Uddén, Hultén, & Hagoort, 2016; Schoffelen et al., 2017). In a large-scale magnetoencephalography (MEG) study, Hultén et al. (2019) investigated visual word integration within a sentence context, focusing on the correlation between distant cortical areas. They found a co-modulation between LIFC and LPTC occurring 400 ms after the onset of each word, across the progression of a sentence. Lam et al. (2016) observed stronger desynchronization of alpha oscillatory activity in frontal and temporal regions for word lists compared to sentences, therefore arguing that oscillatory synchrony between LIFC and LPTC may be crucial for sentence processing. Schoffelen et al. (2017) found bidirectional Granger causal interactions between frontal and posterior temporal regions, where temporal-to-frontal and frontal-to-temporal interactions were supported by alpha and beta oscillatory activity, respectively.

Taken together, these results suggest that different temporal dynamics are at play during sentence and single word processing, and that a dynamic interplay between LIFC and LPTC is important for sentence processing. Accordingly, feedback from LIFC to LPTC may have the functional role of unifying semantic and syntactic representations of single words with high-order semantic and syntactic structures provided by the context (Hultén et al., 2019). My results are consistent with these conclusions, adding evidence to previous findings. Indeed, from previous studies it remained unanswered whether feedback processing from LIPC is necessarily required for language unification. To the best of my knowledge, my work is the first providing direct evidence for a selective role of feedback processing, likely involving frontal areas, in both semantic and syntactic unification.

My work also suggests that frontal and temporal regions within the language network may play different roles in sentence and single word processing, against recent proposals (Fedorenko et al., 2018). In a recent functional magnetic resonance imaging (fMRI) study, Fedorenko et al. (2018) investigated unification and lexical retrieval processes and found no regions that were activated more strongly during unification compared to lexical retrieval. Although some regions showed the opposite pattern (i.e. were more activated by lexical retrieval than by unification), they nevertheless argued that the same regions within the language network are at play during unification and lexical retrieval processes. Their conclusion was that “the language network may be generally more strongly concerned with meaning than structure”. However, even if the same regions subserve unification and lexical retrieval, this does not imply that the same computations are involved in both types of processes. From this perspective, my findings suggest that different computations are performed during unification and lexical retrieval, and that supplementary resources (i.e. feedback from the frontal cortex) may be recruited in order to combine single words into sentences.

One merit of this work is that I tested truly combinatorial mechanisms (both semantic and syntactic), and not simple multiple word integration[31]. In all experiments, in order to perform the task in the unification condition, participants had to combine single words into a new unit. In semantic unification that implied combining single word meanings into a novel, unique meaning. In syntactic unification that involved checking single word structures (e.g. noun-verb agreement) in order to create a well-formed, larger structure (i.e. a sentence or a noun phrase). My results suggest that there may be qualitative differences in unification and lexical retrieval processes, since I found ERP markers of linguistic processing in the

---

[31] This point was extensively discussed in the Discussion (section 3.4.4) of Chapter 3.

masked single word condition[32], but not in the masked unification condition. However, I cannot exclude that results also reflect higher difficulty of unification processes compared to single word processes. As previously noticed[33], in all experiments I aimed to minimize differences between the unification and single word conditions. However, unification processes may be intrinsically harder than single word processing, and this may make it impossible to completely equalize task difficulty in the two cases.

It should be noted that my results do not provide any additional evidence to the debate on which areas of the LIFC subserve semantic and syntactic unification, respectively (Hagoort & Indefrey, 2014; Pallier, Devauchelle, & Dehaene, 2011). In the same way, the present findings add no insights on which routes connect left frontal and temporal areas. LPTC and LIFC are known to be connected, both anatomically (Catani, Jones, & Ffytche, 2005) and functionally (Schoffelen et al., 2017; Xiang et al., 2010), but it is a matter of debate on which exact connections the interplay between LIFC and LPTC relies. It has been argued that feedback processing is provided by the dorsal pathway connecting the posterior IFG (Broca's areas 44/45) to the posterior temporal cortex (Friederici, 2012). This may occur via the superior longitudinal fasciculus (SLF)/arcuate fasciculus (AF), either by a direct route or through an indirect connection mediated by the parietal cortex (Catani et al., 2005). Future work is needed to clarify this point.

Similarly, as previously noticed[34], my work does not provide direct evidence that visual masking specifically impairs feedback processing between the LIFC and the LPTC. Nevertheless, masking has been shown to disrupt long-distance feedback processing from frontal areas to higher visual areas (Del Cul et al., 2009), as well as from higher to lower visual areas (Fahrenfort et al., 2007, 2017; Kovacs et al., 1995; Lamme et al., 2002). Moreover, conscious reportability has been found to be correlated with highly-distributed fronto-temporo-parietal activations (Del Cul et al., 2007). In patients with disorders of consciousness (i.e. coma, vegetative and minimally conscious state), a reduction of long-distance feedback processing from frontal to temporal cortices has been observed (Boly et al., 2011). Taken together, these studies suggest that masking disrupts feedback between distant brain regions (including frontal and temporal areas), which makes it plausible to claim that feedback between the LIFC and the LPTC is also disrupted.

---

[32] At least in the experiments reported in Chapter 2, 3 and 5. No ERP effects were found in the masked condition in the experiment reported in Chapter 4.

[33] See the Discussion (section 3.4.4) of Chapter 3.

[34] See the Discussion (section 3.4.2) of Chapter 3.

6.2.1. Why is LIFC important for language unification?

This work adds evidence to a large amount of studies highlighting the important role of LIFC in language unification. One may thus wonder why LIFC is so crucial for language combinatorial processes. Combinatorial processes are made possible by the ability of combining primitives (i.e. words, but also mathematical symbols) in order to create complex embedded structures (also called trees). These embedded structures involve the recursive employment of the same elements at different levels. It has been suggested that, among primates, humans are the only species that can represent tree structures from sequential data (Dehaene et al., 2015). Fitch gave to this ability the suggestive name of "dendrophilia" (Fitch, 2014).

It has been shown that inferior frontal areas subserve the representation of embedded structures, both linguistic (Makuuchi, Bahlmann, Anwander, & Friederici, 2009; Snijders et al., 2009) and non-linguistic (Reverberi, Görgen, & Haynes, 2012). When processing simple, non-linguistic embedded structures, it seems that inferior frontal areas are uniquely activated in humans compared to other primates (Wang, Uhrig, Jarraya, & Dehaene, 2015). For example, Wang et al. (2015) investigated sequence learning in untrained macaques and humans using fMRI. They recorded brain responses to regular and deviant auditory sequences, which violated the original pattern either in number (e.g. going from AAAB to AAAAB or AB) or in the tone-repetition pattern (e.g. going from AAAB to AAAA or *vice versa*). They found that only in humans bilateral inferior frontal areas showed correlated effects of number and sequence change.

There are anatomical and functional characteristics of inferior frontal areas that make it especially suitable to combinatorial processing. First, inferior frontal areas are more expanded and inter-connected in humans (Mantini, Corbetta, Romani, Orban, & Vanduffel, 2013), and exhibit more connections with auditory associative areas as well (Neubert, Mars, Thomas, Sallet, & Rushworth, 2014). The arcuate fasciculus, i.e. a major white matter tract that connects frontal, parietal and temporal lobes (Catani & Thiebaut de Schotten, 2008), has frontal-to-temporal projections that are uniquely present in humans (Rilling, 2014)[35].

This evolution of inferior frontal cortex may explain why humans are the only species that is able to process tree structures since the first months of life, with-

---

[35] A complete overview of the functional and connectivity differences of frontal areas across human and non-human primates is obviously beyond the goal of this thesis. For a more extensive review, see for example Neubert et al. (2014). For an extensive discussion of the evolution of the language faculty, see the debate that opposes Hauser, Chomsky and Fitch (Fitch, Hauser, & Chomsky, 2005; Hauser, Chomsky, & Fitch, 2002) to Pinker and Jackendoff (Jackendoff & Pinker, 2005; Pinker & Jackendoff, 2005).

out considerable training and prior to education (Marcus, Vijayan, Bandi Rao, & Vishton, 1999). This account entails that inferior frontal areas are not only important for language combinatorial processes, but for generally encoding abstract combinatorial properties that are necessary for linguistic, mathematical and musical representations – all abilities that uniquely distinguish humans from all other species in the animal kingdom.

6.2.2. Why is feedback processing required for language unification?

One main finding of this thesis is that feedback processing may be crucially involved in language unification, both at the semantic and the syntactic level. First, I acknowledge that drawing conclusions from a null result is always a risky operation. However, in my experiments, I associated the lack of an effect in the masked unification condition with the presence of an effect in the masked single word condition[36]. Moreover, in the unmasked condition, an effect was clearly present in both the unification and the single word condition. To the best of my knowledge, my work is the first that has the merit to combine unmasked/masked unification and single word processing within the same experimental paradigm.

Why is feedback processing crucial for unification? An account of semantic unification has been developed based on neurophysiological constraints (Baggio & Hagoort, 2011; Ballard, Hayhoe, Pook, & Rao, 1997; Hagoort, 2017). When the flow of a sentence starts to be encoded, lexical information is treated in the first place. This is mainly done by neurons in temporal regions (Schoffelen et al., 2017; Turken & Dronkers, 2011). First, low-level lexical features of words are encoded (e.g. word frequency), followed by higher-level features, including semantic constraints (e.g. the article *the* should be followed by a noun, or by the other elements composing the noun phrase). Next, local connectivity within temporal areas is established, which codes for lexical features of words (e.g. for the word *ball*: size, color, etc.). Thanks to a second connectivity route, probably involving white matter fronto-temporal connections, the input is then transferred from temporal to frontal areas. Frontal neurons are also activated at this point. However, frontal areas do not subserve long-term memory storage (Simons & Spiers, 2003)[37], hence local connectivity may not be able to be established there. Therefore, crucially, the input needs to be sent back to temporal areas. The most convenient option is that this happens through the same regions that first sent it to frontal areas (Ballard et al., 1997). This creates another spread of activation within the

---

[36] Except for the experiment described in Chapter 4. I discussed the reasons why in this case we did not find an effect in the masked single word condition in the Discussion of Chapter 4 and 5.

[37] However, frontal areas *are* thought to subserve working memory (Baldo & Dronkers, 2006).

temporal cortex, thanks to which the connections representing semantic constraints (i.e. context) are activated. This process establishes cycles of recurrent activation between frontal and temporal areas.

According to this account, feedback processing is crucial from a functional point of view, in order to establish and maintain active a semantic context, and therefore to build sentence meaning over time. In the experiments described here, masking disrupted feedback processing, and this prevented context creation to occur. This may explain why no effect of unification processing was found under the masked condition.

Note that this account does not suggest that there is a magic moment in time in which word processing is completed in frontal areas, then fed back to temporal areas. According to the magic moment hypothesis (Balota & Yap, 2006), there is an instant in which lexical identification takes place, and only after that instant access to meaning becomes possible. On the contrary, unification is realized in a dynamic interplay, in which continuous cycles of activity are established between frontal and temporal regions (Hultén et al., 2019). The interaction between high-order language processes and the feedforward visual processing stream is essential to create the context of an in-progress sentence, and this process of context creation is essential for solving the binding problem necessary to unification.

It has been suggested that recurrent processing between frontal and temporal areas may be essential for neurophysiological reasons (Baggio & Hagoort, 2011; Hagoort, 2017). Neurotransmitters have different decay times, according to which they may play different functional roles. Feedforward processing is usually quite fast, hence is thought to be mediated by fast AMPA and $GABA_A$ receptors. Feedback processing, which is slower, is subserved by slower receptors, i.e. NMDA receptors (Friston, 2005; Garrido et al., 2007). NMDA receptors are thought to be crucial for information maintenance in working memory (Lisman, Fellous, & Wang, 1998). As noticed above, information maintenance is also an important component of semantic unification (Baggio & Hagoort, 2011), hence NMDA-mediated feedback processing may be crucially involved in semantic unification in order to keep semantic context active over time. However, although interesting, this neurophysiological explanation is speculative and not yet supported by data. Future empirical work is needed in this direction.

It should be noted that this account only holds for semantic unification. Some theoretical and empirical work has been done to investigate the role of feedback in syntactic unification (Snijders et al., 2009). However, more work is needed to elaborate a theoretical account of syntactic unification, especially for what concerns its neurophysiological bases. Moreover, future studies should explore the role of feedback processing in phonological unification.

6.3. Implications and outlook for N400 accounts

As described in the Introduction[38], two opposing views within the language literature aim to explain the N400 effect[39]. On the one hand, integration accounts associate the N400 effect with controlled aspects of the linguistic analysis (Baggio & Hagoort, 2011; Kutas & Hillyard, 1980). Accordingly, in manipulations at the sentence (or at the multiple word) level, the N400 effect reflects the integration of a critical word within the current context. This view is supported by a wide literature finding N400 effects at the post-lexical level (e.g. combinatorial or pragmatic level). The MUC model stays on this side of the debate. Here, the N400 effect is described as a marker of recurrent processing, reflecting recurrent activity within the fronto-temporal network (Baggio & Hagoort, 2011; Hagoort, 2017). From this perspective, feedback processing may be needed for N400 effects to occur. On the other hand, lexical frameworks link the N400 effect to lexical access, thus explaining it as a non-combinatorial and automatic phenomenon. This view is justified by the presence of N400 responses at early, pre-lexical steps (e.g. processing of lexical frequency or ortographic similarity).

In Chapter 2 and 3, I have shown that N400 effects do not necessarily reflect recurrent processing, since these effects were still present when disrupting feedback with masking (at least in the single word condition). This may be problematic for integration theories. At the same time, N400 effects under the masked condition were affected by feedback disruption, being significantly reduced in the masked condition compared to the unmasked condition. This may be an issue for lexical theories. Overall, this highlights that the integration-lexical dichotomy may just be problematic in itself, as none of the two views fully accounts for the nature of the N400 effect. Similar criticisms against the current state of the debate have been raised in the past years (Kutas & Federmeier, 2010).

An element that may help to reframe the debate is considering that N400 generators are located within both the frontal and temporal cortex. Taking masked and unmasked processing as an example, that may mean that the masked N400 effect is generated by the temporal cortex only, whereas both frontal and temporal cortex contribute to the effect during unmasked processing. This may also explain why the N400 effect to single words is reduced during masked processing. This is consistent with the idea that the N400 is sensitive to the influence

---

[38] See **Box 2**.

[39] See the reviews by Kutas and Federmaier (2010) and Lau et al. (2008).

of automatic semantic priming (Batterink et al., 2010), but does not reflect automatic or controlled processing in itself. This was also highlighted by Kutas & Federmeier (2010): “The N400 could not be neatly mapped onto the automatic or controlled category, having characteristics associated with each (being importantly modulated by selective attention, and thus not fully automatic, but not requiring the kind of awareness important for controlled processing)”. Accordingly, “the N400 region of the ERP is more accurately described as reflecting the activity in a multimodal long-term memory system that is induced by a given input stimulus during a delimited time window as meaning is dynamically constructed” (Kutas & Federmeier, 2010).

6.4. Implications and outlook for masked semantic/syntactic priming

My results shed some light on the nature of cognitive processing under reduced levels of awareness. There is currently a heated debate on the limits of unconscious processing[40] (Mudrik, Breska, Lamy, & Deouell, 2011; Rohaut & Naccache, 2018), with some authors proposing that many high-level cognitive functions can be performed unconsciously (Hassin, 2013), while others claim that unconscious processing is rather limited in scope (Hesselmann & Moors, 2015). Providing a solution to this issue is a central challenge for cognitive neuroscience, since disentangling processes that can occur unconsciously from those that need conscious awareness is a necessary step towards defining the functional role of consciousness (Baars, 1988)[41]. Moreover, understanding the limits of unconscious cognition is of primary importance from the clinical point of view, in order to provide better diagnoses of residual cognition in patients with disorders of consciousness (Coleman et al., 2007; Cruse et al., 2014; Rohaut & Naccache, 2018).

It is widely accepted that early visual processing (e.g. processing of orientation and color) can occur unconsciously (Boyer, Harrison, & Ro, 2005). The last

---

[40] Note that there is a difference between “unconscious processing” and “processing under reduced levels of awareness”. In the first case, cognitive processing is meant to be fully unconscious, whereas in the second case it can either be fully or partially unconscious. When a stimulus is processed in a fully unconscious fashion, activation is described as weak, only feedforward and limited to posterior sensory regions. During partially conscious processing, local recurrent processing may also be present (Dehaene et al., 2006). See section 1.6 of the Introduction on this topic.

[41] This argument assumes that consciousness has a functional role. Against functionalist stances on consciousness (Baars, 1988; Tononi & Edelman, 1998, just to cite two influential neurocognitive models), there are authors proposing that consciousness is an epiphenomenon of physical events occurring in the brain, and has no causal impact on other physical events occurring in and outside the brain (e.g. Chalmers, 1996; Jackson, 1982; Velmans, 1991). An extensive review of the debate pro and against functionalism is obviously beyond the scope of this thesis. For an overview, see for example Block (2009).

decades have seen an increasing number of studies suggesting that many high-level cognitive processes, from cognitive control (Lau & Passingham, 2007; van Gaal, Ridderinkhof, Scholte, & Lamme, 2010) to error detection (Charles, Van Opstal, Marti, & Dehaene, 2013) and reasoning (Todd, Molden, Ham, & Vonk, 2011), can occur unconsciously as well. This also holds for language processing. Recent studies have suggested that priming may occur not only at the single word level (i.e. prime is one word, Kouider & Dehaene, 2007), but also for multiple words (Armstrong & Dienes, 2013; van Gaal et al., 2014) and entire sentences (Armstrong & Dienes, 2014; Hung & Hsieh, 2015; Nakamura et al., 2018; Sklar et al., 2012). However, at least in some of the studies on language-related unconscious priming, one can question the validity of the conclusions regarding the fully unconscious character of the primes, as well as the genuinely semantic nature of the effects[42].

6.4.1. Is masked semantic/syntactic priming really unconscious?

As explained in the Introduction[43], a proof of unconscious perception relies on the dissociation between a direct and an indirect measure of awareness (Reingold & Merikle, 1988). The direct measure (in which performance is at chance level, e.g. discrimination task) indicates that stimulus information is unavailable to consciousness. The indirect measure (in which performance is above chance level, e.g. ERPs or reaction times) indicates that this unconscious stimulus information may nevertheless influence cognitive processes. Therefore, an objective awareness check (direct measure) should always be associated to the indirect measure in order to exclude that the prime is partially perceived. Most studies on masked semantic/syntactic priming now include this objective awareness check. However, since aggregate awareness is often better than chance, a common practice relies on post-hoc exclusion of subjects that show above-chance performance in the direct measure of perception (Shanks, 2017). A recent study by Shanks (2017) suggests that this practice may be flawed, for issues related to the regression to the mean.

In my studies, in most cases awareness measures were slightly above chance in the masked condition. As previously discussed[44], that may be because participants were aware that primes were present, but not clearly perceivable. However, since in my work I focused on showing the absence of an effect in the masked uni-

---

[42] In the following paragraphs, I will mostly refer to studies on masked semantic priming, as very few studies have investigated masked syntactic priming. It is reasonable to speculate that similar considerations hold for masked syntactic priming.

[43] See **Box 3**.

[44] See the Discussion (section 3.4.3) of Chapter 3.

fication condition, potentially partial awareness does not represent a major issue. This may be more problematic for studies that claim to prove full unconscious priming and in which, still, p-values of the direct measure (e.g. in the discrimination task) are significant or marginally significant (e.g. Berkovitch & Dehaene, 2019).

6.4.2. Is masked semantic/syntactic priming really language-related?

My work shows that masked processing abolishes unification mechanisms, against studies claiming that high-level linguistic processing can be performed under reduced levels of awareness (Armstrong & Dienes, 2014; Berkovitch & Dehaene, 2019; Iijima & Sakai, 2014; Nakamura et al., 2018; Sklar et al., 2012). Moreover, the results in the masked single word condition suggest that masked single word processing is strongly influenced by experimental factors.

In a large meta-analysis, Van den Bussche et al. (2009) indicate three experimental parameters that may influence priming effects in semantic categorization tasks (e.g. animacy or relatedness categorization)[45]: stimulus onset asynchrony (SOA)[46], category size, and prime novelty. First, it has been shown that semantic priming decreases at long SOAs (Greenwald et al., 1996; Kiefer & Spitzer, 2000). The results reported in Chapter 2 confirm this observation, since I only found an ERP effect in masked words occurring at the shortest SOA.

Second, some studies have only found priming effects when stimuli are members of small categories (e.g. body parts or numbers). When larger categories (e.g. animals) were employed, priming was not observed (Forster, 2004; Forster, Mohan, & Hector, 2003), suggesting that priming may decrease when category size increases. When stimulus category is sufficiently small, observed priming may have a non-semantic explanation, as in this case participants may form action triggers for the stimuli that they receive as input during the experiment (Kunde, Kiesel, & Hoffmann, 2003). For example, if the task is a number categorization task (e.g. categorize a number as larger or smaller than 5), participants prepare themselves by forming action triggers with all numbers between 1 and 9, which allows them to respond without processing targets semantically. This is less likely to occur when stimulus category is large. In the experiments reported in Chapter 2 and 3, only eight words (four nouns and four verbs) were presented as primes. They did not belong to a small category, but participants were familiarized with all

---

[45] According to Van den Bussche et al. (2009), lexical decision tasks are affected by different factors, i.e. sample size, target set size, prime duration, and the presence of an objective awareness check.

[46] SOA is the time from mask onset to target onset.

stimuli before the task and, in addition, underwent a training session before the main EEG task. Therefore, the action trigger hypothesis may explain the effect in the masked single word condition.

Third, when the same words are employed as primes and targets, participants may learn to associate word pairs directly with correct responses, forming automatic stimulus-response mappings that circumvent the semantic analysis (Damian, 2001). Accordingly, priming may decrease with prime novelty. As previously noticed[47], this may explain why I did not find any masked single word effect in the experiment reported in Chapter 4 (in which primes and targets belonged to different lists), and why, on the contrary, I found a masked priming effect in the following experiment, reported in Chapter 5 (in which primes and targets belonged to the same list).

It has been claimed that visual similarity between primes and targets (e.g. orthographic overlap) may also trigger non-semantic masked priming effects (Abrams, 2008; Abrams & Greenwald, 2000). For example, Abrams & Greenwald (2000) showed that the word *smile* may be classified as a negative masked prime after repeated classification of *smut* and *bile* (that partially overlap with *smile* on the orthographic point of view). One way of avoiding this issue is employing prime-target pairs that belong to different formats (e.g. word-picture pairs), in order to rule out the visual similarity explanation. In the experiments reported in Chapter 2 and 3, I fulfilled this criterion, as words and pictures were employed as primes and targets, respectively.

In summary, in order to prove genuine unconscious semantic priming, several criteria should be met[48]: (i) objective awareness check; (ii) prime novelty; (iii) large stimulus set; and (iv) control of visual similarity. To the best of my knowledge, not many studies showed clear evidence of unconscious semantic priming while fulfilling all these requirements. Moreover, findings were not always replicable. For example, in a study by Van den Bussche et al. (2009), target words (animals or objects) were preceded by pictures of animals or objects. Subjects performed an animal/non-animal categorization task. Results showed that reaction times (RTs) were faster for congruent picture-word pairs compared to incongruent pairs. However, these findings recently failed replication (Stein et al., 2018). This may be due to the rather long SOA employed in both the original study and the replication (i.e. 290 ms), even if this does not explain why an effect was nevertheless found in the original study. Future attempts of replication should take this into account, and try to replicate Van den Bussche et al.'s study while employing shorter SOAs.

---

[47] See the Discussion of Chapter 4 and 5.

[48] For a similar argument, see Stein et al. (2018).

Overall, the work reported in this thesis suggests that masked processing of linguistic stimuli (even if partially and not fully unconscious) is rather limited in scope, and that conscious and unconscious processing may subserve very different cognitive functions. Moreover, my studies add evidence to an increasing body of work challenging the existence of masked semantic priming that is purely unconscious and purely semantic. Future studies on masked priming should clarify this issue. From this perspective, an effort should be done in order to minimize as much as possible the differences between experimental settings, stimulus sets, and measuring techniques across different studies.

6.5. Conclusion

The studies that I have reported in this thesis show that long-range feedback processing, likely involving frontal areas, is required for semantic and syntactic unification, but not for lexical retrieval. When disrupting feedback with visual masking, which reduces stimulus awareness, unification mechanisms were impaired, while lexical retrieval mechanisms were spared (at least until a certain extent). Therefore, language combinatorial processes, both at the semantic and the syntactic level, may require full awareness, whereas single word processing may occur under reduced levels of awareness. This implies that distinct brain mechanisms may be involved in sentence and single word processing, adding new insights to ongoing debates about the specific roles of different brain mechanisms in a distributed language network (Goucha & Friederici, 2015; Hagoort, 2017; Hickok & Poeppel, 2007; Thompson-Schill, Bedny, & Goldberg, 2005). This work hopefully provides a valid contribution to the scientific effort of understanding the most unique capacity of human language faculty: the power of creating worlds with words.

References

Abrams, R. L. (2008). Orthographic overlap and category size in unconscious category priming. Comment on Experiment 1c of Van den Bussche and Reynvoet (2007). *Experimental Psychology*, *55*(5),350–357. https://doi.org/10.1027/1618-3169.55.5.350

Abrams, R. L., & Greenwald, A. G. (2000). Parts outweigh the whole (word) in unconscious analysis of meaning. *Psychological Science*, *11*(2), 118–124. https://doi.org/10.1111/1467-9280.00226

Abrams, R. L., Klinger, M. R., & Greenwald, A. G. (2002). Subliminal words activate semantic categories (not automated motor responses). *Psychonomic Bulletin and Review*, *9*(1), 100–106. https://doi.org/10.3758/BF03196262

Adger, D. (2018). The Autonomy of Syntax. In N. Hornstein, H. Lasnik, P. Patel-Grosz, C. Yang, & N. Chomsky (Eds.), *Syntactic Structures after 60 Years: The impact of the Chomskian revolution in linguistics* (pp. 153–176). Boston: De Gruyter Mouton. https://doi.org/10.1515/9781501506925-157

Ansorge, U., Reynvoet, B., Hendler, J., Oettl, L., & Evert, S. (2013). Conditional automaticity in subliminal morphosyntactic priming. *Psychological Research*, *77*(4), 399–421. https://doi.org/10.1007/s00426-012-0442-z

Armstrong, A. M., & Dienes, Z. (2013). Subliminal understanding of negation: Unconscious control by subliminal processing of word pairs. *Consciousness and Cognition*, *22*, 1022–1040. https://doi.org/10.1016/j.concog.2013.06.010

Armstrong, A. M., & Dienes, Z. (2014). Subliminal understanding of active versus passive sentences. *Psychology of Consciousness: Theory, Research, and Practice*, *1*(1), 32–50. https://doi.org/10.1037/css0000002

Avneon, M., & Lamy, D. (2019). Do semantic priming and retrieval of stimulus-response associations depend on conscious perception? *Consciousness and Cognition*, *69*, 36–51. https://doi.org/10.1016/j.concog.2019.01.010

Axelrod, V., Bar, M., Rees, G., & Yovel, G. (2015). Neural Correlates of Subliminal Language Processing. *Cerebral Cortex*, *25*(8), 2160–2169. https://doi.org/10.1093/cercor/bhu022

Baars, B. J. (1988). *A cognitive theory of consciousness*. Cambridge, MA: Cambridge University Press.

Baars, B. J., & Franklin, S. (2003). How conscious experience and working memory interact. *Trends in Cognitive Sciences*, *7*(4), 166–172. https://doi.org/10.1016/S1364-6613(03)00056-1

Baggio, G., & Hagoort, P. (2011). The balance between memory and unification in semantics: A dynamic account of the N400. *Language and Cognitive Processes*,*26*(9), 1338–1367. https://doi.org/10.1080/01690965.2010.542671

Baldo, J. V., & Dronkers, N. F. (2006). The role of inferior parietal and inferior frontal cortex in working memory. *Neuropsychology*, *20*(5), 529–538. https://doi.org/10.1037/0894-4105.20.5.529

Ballard, D. H., Hayhoe, M. M., Pook, P. K., & Rao, R. P. N. (1997). Deictic codes for the embodiment of cognition. *Behavioral and Brain Sciences*, *20*(4), 723–742. https://doi.org/10.1017/S0140525X97001611

Balota, D. A., & Yap, M. J. (2006). Attentional control and the flexible lexical processor: Explorations of the magic moment of word recognition. *From Inkmarks to Ideas: Current Issues in Lexical Processing*, 229–258. https://doi.org/10.4324/9780203841211

Bastuji, H., Perrin, F., & Garcia-Larrea, L. (2002). Semantic analysis of auditory input during sleep: Studies with event related potentials. *International Journal of Psychophysiology*, *46*(3), 243–255. https://doi.org/10.1016/S0167-8760(02)00116-2

Batterink, L., Karns, C. M., Yamada, Y., & Neville, H. (2010). The role of awareness in semantic and syntactic processing: An ERP attentional blink study. *Journal of Cognitive Neuroscience*, *22*(11), 2514–2529. https://doi.org/10.1162/jocn.2009.21361

Batterink, L., & Neville, H. J. (2013). The Human Brain Processes Syntax in the Absence of Conscious Awareness. *Journal of Neuroscience*, *33*(19), 8528–8533. https://doi.org/10.1523/jneurosci.0618-13.2013

Berkovitch, L., & Dehaene, S. (2019). Subliminal syntactic priming. *Cognitive Psychology*, *109*, 26–46. https://doi.org/10.1016/j.cogpsych.2018.12.001

Beyersmann, E., Iakimova, G., Ziegler, J. C., & Colé, P. (2014). Semantic processing during morphological priming: An ERP study. *Brain Research*, *1579*, 45–55. https://doi.org/10.1016/j.brainres.2014.07.010

Blalock, L. D. (2013). Mask similarity impacts short-term consolidation in visual working memory. *Psychonomic Bulletin and Review*, *20*(6), 1290–1295. https://doi.org/10.3758/s13423-013-0461-9

Block, N. (2009). Comparing the major theories of consciousness. In M. S. Gazzaniga, E. Bizzi, L. M. Chalupa, S. T. Grafton, T. F. Heatherton, C. Koch, … B. A. Wandell (Eds.), *The cognitive neurosciences* (pp. 1111–1122). Cambridge, MA: Massachusetts Institute of Technology.

Boly, M., Garrido, M. I., Gosseries, O., Bruno, M., Boveroux, P., Schnakers, C., … Friston, K. (2011). Preserved Feedforward But Impaired Top-Down Processes in The Vegetative State. *Science*, *332*, 858–863.

Boly, M., Perlbarg, V., Marrelec, G., Schabus, M., Laureys, S., Doyon, J., … Benali, H. (2012). Hierarchical clustering of brain activity during human nonrapid eye movement sleep. *Proceedings of the National Academy of Sciences*, *109*(15), 5856–5861. https://doi.org/10.1073/pnas.1111133109

Boyer, J. L., Harrison, S., & Ro, T. (2005). Unconscious processing of orientation and color without primary visual cortex. *Proceedings of the National Academy of Sciences*, *102*(46), 16875–16879. https://doi.org/10.1167/5.8.285

Breitmeyer, B. G., & Ogmen, H. (2000). Recent models and findings in visual backward masking: A comparison, review, and update. *Perception and Psychophysics*, *62*(8), 1572–1595. https://doi.org/10.3758/BF03212157

Brouwer, H., Crocker, M. W., Venhuizen, N. J., & Hoeks, J. C. J. (2017). A Neurocomputational Model of the N400 and the P600 in Language Processing. *Cognitive Science*, *41*(6), 1318–1352. https://doi.org/10.1111/cogs.12461

Brown, C., & Hagoort, P. (1993). The processing nature of the N400: Evidence from masked priming. *Journal of Cognitive Neuroscience*, *5*(1), 34–44. https://doi.org/10.1162/jocn.1993.5.1.34

Brualla, J., Romero, M. F., Serrano, M., & Valdizan, J. R. (1998). Auditory Event-related Potentials to Semantic Priming During Sleep. *Electroencephalography and Clinical Neurophysiology*, *108*, 283–290.

Catani, M., Allin, M. P. G., Husain, M., Pugliese, L., Mesulam, M. M., Murray, R. M., & Jones, D. K. (2007). Symmetries in human brain language pathways correlate with verbal recall. *Proceedings of the National Academy of Sciences*, *104*(43), 17163–17168. https://doi.org/10.1073/pnas.0702116104

Catani, M., Jones, D. K., & Ffytche, D. H. (2005). Perisylvian language networks of the human brain. *Annals of Neurology*, *57*, 8–16. https://doi.org/10.1002/ana.20319

Catani, M., & Thiebaut de Schotten, M. (2008). A diffusion tensor imaging tractography atlas for virtual in vivo dissections. *Cortex*, *44*(8), 1105–1132. https://doi.org/10.1016/j.cortex.2008.05.004

Chalmers, D. (1996). *The conscious mind*. Oxford: Oxford University Press.

Charles, L., Van Opstal, F., Marti, S., & Dehaene, S. (2013). Distinct brain mechanisms for conscious versus subliminal error detection. *NeuroImage*, *73*, 80–94. https://doi.org/10.1016/j.neuroimage.2013.01.054

Chomsky, N. (1957). *Syntactic structures*. The Hague: Mouton.

Coco, M. I., Araujo, S., & Petersson, K. M. (2017). Disentangling stimulus plausibility and contextual congruency: Electro-physiological evidence for differential cognitive dynamics. *Neuropsychologia*, *96*, 150–163. https://doi.org/10.1016/j.neuropsychologia.2016.12.008

Coleman, M. R., Rodd, J. M., Davis, M. H., Johnsrude, I. S., Menon, D. K., Pickard, J. D., & Owen, A. M. (2007). Do vegetative patients retain aspects of language comprehension? Evidence from fMRI. *Brain*, *130*(10), 2494–2507. https://doi.org/10.1093/brain/awm170

Cruse, D., Beukema, S., Chennu, S., Malins, J. G., Owen, A. M., & McRae, K. (2014). The reliability of the N400 in single subjects: Implications for patients with disorders of consciousness. *NeuroImage: Clinical*, *4*, 788–799. https://doi.org/10.1016/j.nicl.2014.05.001

Cutler, A., & Clifton, C. (1999). Comprehending spoken language: A blueprint of the listener. In C. M. Brown & P. Hagoort (Eds.), *The Neurocognition of Language* (pp. 123–166). Oxford: Oxford University Press.

Daltrozzo, J., Claude, L., Tillmann, B., Bastuji, H., & Perrin, F. (2012). Working Memory Is Partially Preserved during Sleep. *PLoS ONE*, *7*(12), 1–12. https://doi.org/10.1371/journal.pone.0050997

Damian, M. F. (2001). Congruity Effects Evoked by Subliminally Presented Primes. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 154–165.

Davis, M. H., Coleman, M. R., Absalom, A. R., Rodd, J. M., Johnsrude, I. S., Matta, B. F., … Menon, D. K. (2007). Dissociating speech perception and comprehension at reduced levels of awareness. *Proceedings of the National Academy of Sciences*, *104*(41), 16032–16037. https://doi.org/10.1073/pnas.0701309104

Deacon, D., Dynowska, A., Ritter, W., & Grose-Fifer, J. (2004). Repetition and semantic priming of nonwords: Implications for theories of N400 and word recognition. *Psychophysiology*, *41*, 60–74. https://doi.org/10.1111/1469-8986.00120

Deacon, D., Hewitt, S., Yang, C. M., & Nagata, M. (2000). Event-related potential indices of semantic priming using masked and unmasked words: Evidence that the N400 does not reflect a post-lexical process. *Cognitive Brain Research*, *9*(2), 137–146. https://doi.org/10.1016/S0926-6410(99)00050-6

Dehaene, S., & Changeux, J.-P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, *70*(2), 200–227. https://doi.org/10.1016/j.neuron.2011.03.018

Dehaene, S., Changeux, J. P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Sciences*, *10*(5), 204–211. https://doi.org/10.1016/j.tics.2006.03.007

Dehaene, S., Meyniel, F., Wacongne, C., Wang, L., & Pallier, C. (2015). The Neural

Representation of Sequences: From Transition Probabilities to Algebraic Patterns and Linguistic Trees. *Neuron*, *88*(1), 2–19. https://doi.org/10.1016/j.neuron.2015.09.019

Del Cul, A., Baillet, S., & Dehaene, S. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *PLoS Biology*, *5*(10), 2408–2423. https://doi.org/10.1371/journal.pbio.0050260

Del Cul, A., Dehaene, S., Reyes, P., Bravo, E., & Slachevsky, A. (2009). Causal role of prefrontal cortex in the threshold for access to consciousness. *Brain*, *132*(9), 2531–2540. https://doi.org/10.1093/brain/awp111

Deutsch, A., Frost, R., & Forster, K. I. (1998). Verbs and nouns are organized and accessed differently in the mental lexicon: Evidence from Hebrew. *Journal of Experimental Psychology: Learning Memory and Cognition*, *24*(5), 1238–1255. https://doi.org/10.1037/0278-7393.24.5.1238

Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. F. (2007). Masking Disrupts Reentrant Processing in Human Visual Cortex. *Journal of Cognitive Neuroscience*, *19*(9), 1488–1497. https://doi.org/10.1162/jocn.2007.19.9.1488

Fahrenfort, J. J., van Leeuwen, J., Olivers, C. N. L., & Hogendoorn, H. (2017). Perceptual integration without conscious access. *Proceedings of the National Academy of Sciences*, *114*(14), 3744–3749. https://doi.org/10.1073/pnas.1617268114

Federmeier, K. D., & Kutas, M. (2001). Meaning and Modality: Influences of Context, Semantic Memory Organization, and Perceptual Predictability on Picture Processing. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *27*(1), 202–224.

Fedorenko, E., Mineroff, Z., Siegelman, M., & Blank, I. (2018). Word meanings and sentence structure recruit the same set of fronto-temporal regions during comprehension. *BioRxiv [Preprint]*. https://doi.org/https://doi.org/10.1101/477851

Ferreira, F., & Clifton, C. (1986). The independence of syntactic processing. *Journal of Memory and Language*, *25*(3), 348–368. https://doi.org/10.1016/0749-596X(86)90006-9

Fitch, W. T. (2014). Toward a computational framework for cognitive biology: unifying approaches from cognitive neuroscience and comparative cognition. *Physics of Life Reviews*, *11*(3), 329–364. https://doi.org/10.1016/j.plrev.2014.04.005

Fitch, W. T., Hauser, M. D., & Chomsky, N. (2005). The evolution of the language faculty: Clarifications and implications. *Cognition*, *97*, 179–210.

https://doi.org/10.1016/j.cognition.2005.02.005

Forster, K. I. (2004). Category size effects revisited: Frequency and masked priming effects in semantic categorization. *Brain and Language*, *90*, 276–286. https://doi.org/10.1016/S0093-934X(03)00440-1

Forster, K. I., Mohan, K., & Hector, J. (2003). The mechanics of masked priming. In S. Kinoshita & S. J. Lupker (Eds.), *Masked priming: The state of the art* (pp. 3–37). New York: Psychology Press.

Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences*, *6*(2), 78–84. https://doi.org/10.1016/S1364-6613(00)01839-8

Friederici, A. D. (2012). The cortical language circuit: From auditory perception to sentence comprehension. *Trends in Cognitive Sciences*, *16*(5), 262–268. https://doi.org/10.1016/j.tics.2012.04.001

Friederici, A. D., Opitz, B., & Von Cramon, D. Y. (2000). Segregating semantic and syntactic aspects of processing in the human brain: An fMRI investigation of different word types. *Cerebral Cortex*, *10*(7), 698–705. https://doi.org/10.1093/cercor/10.7.698

Friederici, A. D., Pfeifer, E., & Hahne, A. (1993). Event-related brain potentials during natural speech processing: effects of semantic, morphological and syntactic violations. *Cognitive Brain Research*, *1*, 183–192. https://doi.org/https://doi.org/10.1016/0926-6410(93)90026-2

Friederici, A. D., Rueschemeyer, S.-A., Hahne, A., & Fiebach, C. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension. *Cerebral Cortex*, *13*, 170–177.

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*, 815–836. https://doi.org/10.1098/rstb.2005.1622

Garrido, M. I., Kilner, J. M., Kiebel, S. J., & Friston, K. J. (2007). Evoked brain responses are generated by feedback loops. *Proceedings of the National Academy of Sciences*, *104*(52), 20961–20966. https://doi.org/10.1073/pnas.0706274105

Garrido, M. I., Kilner, J. M., Stephan, K. E., & Friston, K. J. (2009). The mismatch negativity: A review of underlying mechanisms. *Clinical Neurophysiology*, *120*(3), 453–463. https://doi.org/10.1016/j.clinph.2008.11.029

Goucha, T., & Friederici, A. D. (2015). The language skeleton after dissecting meaning: A functional segregation within Broca’s Area. *NeuroImage*, *114*, 294–302. https://doi.org/10.1016/j.neuroimage.2015.04.011

Gouvea, A. C., Phillips, C., Kazanina, N., & Poeppel, D. (2010). The linguistic processes underlying the P600. *Language and Cognitive Processes*, *25*(2), 149–188. https://doi.org/10.1080/01690960902965951

Greenwald, A. G., Draine, S. C., & Abrams, R. L. (1996). Three cognitive markers of unconscious semantic activation. *Science*, *273*, 1699–1702. https://doi.org/10.1126/science.273.5282.1699

Hagoort, P. (2005). On Broca, brain, and binding: A new framework. *Trends in Cognitive Sciences*, *9*(9), 416–423. https://doi.org/10.1016/j.tics.2005.07.004

Hagoort, P. (2013). MUC (Memory, Unification, Control) and beyond. *Frontiers in Psychology*, *4*(416), 1–13. https://doi.org/10.3389/fpsyg.2013.00416

Hagoort, P. (2014). Nodes and networks in the neural architecture for language: Broca's region and beyond. *Current Opinion in Neurobiology*, *28*, 136–141. https://doi.org/10.1016/j.conb.2014.07.013

Hagoort, P. (2017). The core and beyond in the language-ready brain. *Neuroscience and Biobehavioral Reviews*, *37*, 347–362. https://doi.org/10.1016/j.neubiorev.2017.01.048

Hagoort, P., Baggio, G., & Willems, R. M. (2009). Semantic Unification. In M. Gazzaniga (Ed.), *The Cognitive Neurosciences* (4th ed., pp. 819–836). Cambridge, MA: MIT Press. https://doi.org/10.1007/978-3-642-54789-8_1

Hagoort, P., Brown, C., & Groothusen, J. (1993). The syntactic positive shift (sps) as an erp measure of syntactic processing. *Language and Cognitive Processes*, *8*(4), 439–483. https://doi.org/10.1080/01690969308407585

Hagoort, P., & Indefrey, P. (2014). The Neurobiology of Language Beyond Single Words. *Annual Review of Neuroscience*, *37*(1), 347–362. https://doi.org/10.1146/annurev-neuro-071013-013847

Hagoort, P., Wassenaar, M., & Brown, C. (2003). Real-time semantic compensation in patients with agrammatic comprehension: Electrophysiological evidence for multiple-route plasticity. *Proceedings of the National Academy of Sciences*, *100*(7), 4340–4345. https://doi.org/10.1073/pnas.0230613100

Hassin, R. R. (2013). Yes It Can: On the Functional Abilities of the Human Unconscious. *Perspectives on Psychological Science*, *8*(2), 195–207. https://doi.org/10.1177/1745691612460684

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science*, *298*, 1569–1579. https://doi.org/10.1126/science.298.5598.1569

Hesselmann, G., & Moors, P. (2015). Definitely maybe: Can unconscious processes perform the same functions as conscious processes? *Frontiers in Psychology*, *6*(584), 1–5. https://doi.org/10.3389/fpsyg.2015.00584

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, *8*, 393–402. https://doi.org/10.1038/nrn2113

Holcomb, P. J., Reder, L., Misra, M., & Grainger, J. (2005). The effects of prime visibility on ERP measures of masked priming. *Cognitive Brain Research*, *24*(1), 155–172. https://doi.org/10.1016/j.cogbrainres.2005.01.003

Hultén, A., Schoffelen, J.-M., Uddén, J., Lam, N. H. L., & Hagoort, P. (2019). How the brain makes sense beyond the processing of single words – An MEG study. *NeuroImage*, *186*, 586–594. https://doi.org/10.1016/j.neuroimage.2018.11.035

Hung, S. M., & Hsieh, P. J. (2015). Syntactic processing in the absence of awareness and semantics. *Journal of Experimental Psychology: Human Perception and Performance*, *41*(5), 1376–1384. https://doi.org/10.1037/xhp0000094

Ibáñez, A., López, V., & Cornejo, C. (2006). ERPs and contextual semantic discrimination : Degrees of congruence in wakefulness and sleep. *Brain and Language*, *98*, 264–275. https://doi.org/10.1016/j.bandl.2006.05.005

Iijima, K., & Sakai, K. L. (2014). Subliminal enhancement of predictive effects during syntactic processing in the left inferior frontal gyrus: an MEG study. *Frontiers in Systems Neuroscience*, *8*, 1–14. https://doi.org/10.3389/fnsys.2014.00217

Jackendoff, R. (2002). *Foundations of Language: Brain, Meaning, Grammar, Evolution*. New York: Oxford University Press.

Jackendoff, R. (2007). A Parallel Architecture perspective on language processing. *Brain Research*, *1146*(1), 2–22. https://doi.org/10.1016/j.brainres.2006.08.111

Jackendoff, R., & Pinker, S. (2005). The nature of the language faculty and its implications for evolution of language (Reply to Fitch, Hauser, and Chomsky). *Cognition*, *97*, 211–225. https://doi.org/10.1016/j.cognition.2005.04.006

Jackson, F. (1982). Epiphenomenal qualia. *Philosophical Quarterly*, *32*, 127–136.

Jiménez-Ortega, L., Espuny, J., de Tejada, P. H., Vargas-Rivero, C., & Martín-Loeches, M. (2017). Subliminal Emotional Words Impact Syntactic Processing: Evidence from Performance and Event-Related Brain Potentials. *Frontiers in Human Neuroscience*, *11*(192), 1–13. https://doi.org/10.3389/fnhum.2017.00192

Jiménez-Ortega, L., García-Milla, M., Fondevila, S., Casado, P., Hernández-Gutiérrez, D., & Martín-Loeches, M. (2014). Automaticity of higher cognitive functions: Neurophysiological evidence for unconscious syntactic processing of masked words. *Biological Psychology*, *103*, 83–91.

https://doi.org/10.1016/j.biopsycho.2014.08.011

Kang, M.-S., Blake, R., & Woodman, G. F. (2011). Semantic Analysis Does Not Occur in the Absence of Awareness Induced by Interocular Suppression. *Journal of Neuroscience*, *31*(38), 13535–13545. https://doi.org/10.1523/jneurosci.1691-11.2011

Keenan, E. L. (1979). On surface form and logical form. *Studies in the Linguistic Sciences Urbana*, *III*(8), 163–203.

Keuleers, E., Brysbaert, M., & New, B. (2010). SUBTLEX-NL: A new measure for Dutch word frequency based on film subtitles. *Behavior Research Methods*, *42*(3), 643–650. https://doi.org/10.3758/BRM.42.3.643

Kiefer, M. (2002). The N400 is modulated by unconsciously perceived masked words: Further evidence for an automatic spreading activation account of N400 priming effects. *Cognitive Brain Research*, *13*(1), 27–39. https://doi.org/10.1016/S0926-6410(01)00085-4

Kiefer, M., & Brendel, D. (2006). Attentional Modulation of Unconscious “Automatic” Processes: Evidence from Event-related Potentials in a Masked Priming Paradigm. *Journal of Cognitive Neuroscience*, *18*(2), 184–198. https://doi.org/10.1162/jocn.2006.18.2.184

Kiefer, M., & Martens, U. (2010). Attentional sensitization of unconscious cognition: Task sets modulate subsequent masked semantic priming. *Journal of Experimental Psychology: General*, *139*(3), 464–489. https://doi.org/10.1037/a0019561

Kiefer, M., & Spitzer, M. (2000). Time course of conscious and unconscious semantic brain activation. *Neuroreport*, *11*(11), 2401–2407. Retrieved from https://journals.lww.com/neuroreport/Fulltext/2000/08030/Time_course_of_conscious_and_unconscious_semantic.13.aspx

Kiehl, K. A., Laurens, K. R., & Liddle, P. F. (2002). Reading anomalous sentences: An event-related fMRI study of semantic processing. *NeuroImage*, *17*(2), 842–850. https://doi.org/10.1016/S1053-8119(02)91244-9

Kong, L., Zhang, J. X., Kang, C., Du, Y., Zhang, B., & Wang, S. (2010). P200 and phonological processing in Chinese word recognition. *Neuroscience Letters*, *473*(1), 37–41. https://doi.org/10.1016/j.neulet.2010.02.014

Kos, M., Vosse, T., van den Brink, D., & Hagoort, P. (2010). About edible restaurants: Conflicts between syntax and semantics as revealed by ERPs. *Frontiers in Psychology*, *1*(222), 1–11. https://doi.org/10.3389/fpsyg.2010.00222

Kouider, S., & Dehaene, S. (2007). Levels of processing during non-conscious perception: A critical review of visual masking. *Philosophical Transactions of* *the Royal Society B: Biological Sciences*, *362*, 857–875. https://doi.org/10.1098/rstb.2007.2093

Kovacs, G., Vogels, R., Orban, G. A., & Sprague, J. M. (1995). Cortical correlate of pattern backward masking (inferior temporal cortex/temporal integration/shape recognition). *Neurobiology*, *92*, 5587–5591.

Kunde, W., Kiesel, A., & Hoffmann, J. (2003). Conscious control over the content of unconscious cognition. *Cognition*, *88*, 223–242. https://doi.org/10.1016/S0

Kunde, W., Kiesel, A., & Hoffmann, J. (2005). On the masking and disclosure of unconscious elaborate processing. A reply to Van Opstal, Reynvoet, and Verguts (2005). *Cognition*, *97*, 99–105. https://doi.org/10.1016/j.cognition.2005.03.005

Kutas, M., & Federmeier, K. D. (2010). Thirty Years and Counting: Finding Meaning in the N400 Component of the Event-Related Brain Potential (ERP). *Annual Review of Psychology*, *62*, 621–647. https://doi.org/10.1146/annurev.psych.093008.131123

Kutas, M., & Hillyard, S. A. (1980). Event related potentials in response to semantically inappropriate and surprisingly large words. *Biological Psychology*, *11*, 99–116. https://doi.org/http://doi.org/10.1016/0301-0511(80)90046-0

Kutas, M., & Hillyard, S. A. (1984). Brain potentials during reading reflect word expectancy and semantic association. *Nature*, *307*(12), 161–163.

Lam, N. H. L., Schoffelen, J. M., Uddén, J., Hultén, A., & Hagoort, P. (2016). Neural activity during sentence processing as reflected in theta, alpha, beta, and gamma oscillations. *NeuroImage*, *142*, 43–54. https://doi.org/10.1016/j.neuroimage.2016.03.007

Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *10*(11), 494–501. https://doi.org/10.1016/j.tics.2006.09.001

Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, *23*(11), 571–579. https://doi.org/10.1016/S0166-2236(00)01657-X

Lamme, V. A. F., Zipser, K., & Spekreijse, H. (2002). Masking interrupts figure-ground signals in V1. *Journal of Cognitive Neuroscience*, *14*(7), 1044–1053. https://doi.org/10.1162/089892902320474490

Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature Reviews. Neuroscience*, *9*(12), 920–933. https://doi.org/10.1038/nrn2532

Lau, H. C., & Passingham, R. E. (2007). Unconscious Activation of the Cognitive

Control System in the Human Prefrontal Cortex. *Journal of Neuroscience*, *27*(21), 5805–5811. https://doi.org/10.1523/jneurosci.4335-06.2007

Levelt, P. (1992). Accessing words in speech production - Stages, processes and representations. *Cognition*, *42*, 1–22.

Lisman, J. E., Fellous, J. M., & Wang, X. J. (1998). A role for NMDA-receptor channels in working memory. *Nature Neuroscience*, *1*(4), 273–275. https://doi.org/10.1038/1086

Luck, S. J., Vogel, E. K., & Shapiro, K. L. (1996). Word meanings can be accessed but not reported during the attentional blink. *Nature*, *383*(6601), 616–618. https://doi.org/10.1038/383616a0

Makuuchi, M., Bahlmann, J., Anwander, A., & Friederici, A. D. (2009). Segregating the core computational faculty of human language from working memory. *Proceedings of the National Academy of Sciences*, *106*(20), 8362–8367. https://doi.org/10.1073/pnas.0810928106

Mantini, D., Corbetta, M., Romani, G. L., Orban, G. A., & Vanduffel, W. (2013). Evolutionarily Novel Functional Networks in the Human Brain? *Journal of Neuroscience*, *33*(8), 3259–3275. https://doi.org/10.1523/jneurosci.4392-12.2013

Marcel, A. (1980). Conscious and preconscious recognition of polysemous words: locating the selective effects of prior verbal context. In R. S. Nickerson (Ed.), *Attention and performance, VIII*. Hillsdale,NJ: Erlbaum.

Marcus, G. F., Vijayan, S., Bandi Rao, S., & Vishton, P. M. (1999). Rule learning by seven-month-old infants. *Science*, *283*(5398), 77–80. https://doi.org/10.1126/science.283.5398.77

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*(1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024

Massimini, M., Ferrarelli, F., Huber, R., Esser, S. K., Singh, H., & Tononi, G. (2005). Breakdown of Cortical Effective Connectivity During Sleep -- supporting material. *Science*, *309*(5744), 2228–2233. https://doi.org/10.1126/science.1117256

Meijs, E. L., Slagter, H. A., de Lange, F. P., & van Gaal, S. (2018). Dynamic interactions between top-down expectations and conscious awareness. *The Journal of Neuroscience*, *38*(9), 2318–2327. https://doi.org/10.1523/JNEUROSCI.1952-17.2017

Menenti, L., Gierhan, S. M. E., Segaert, K., & Hagoort, P. (2011). Shared language: Overlap and segregation of the neuronal infrastructure for speaking and listening revealed by functional MRI. *Psychological Science*, *22*(9), 1173–

1182. https://doi.org/10.1177/0956797611418347

Mongelli, V., Meijs, E. L., van Gaal, S., & Hagoort, P. (2019). No language unification without neural feedback: How awareness affects sentence processing. *NeuroImage*, *202*, 1–12. https://doi.org/10.1016/j.neuroimage.2019.116063

Mudrik, L., Breska, A., Lamy, D., & Deouell, L. Y. (2011). Integration without awareness: Expanding the limits of unconscious processing. *Psychological Science*, *22*(6), 764–770. https://doi.org/10.1177/0956797611408736

Nakamura, K., Makuuchi, M., Oga, T., Mizuochi-Endo, T., Iwabuchi, T., Nakajima, Y., & Dehaene, S. (2018). Neural capacity limits during unconscious semantic processing. *European Journal of Neuroscience*, *47*(8), 929–937. https://doi.org/10.1111/ejn.13890

Neubert, F. X., Mars, R. B., Thomas, A. G., Sallet, J., & Rushworth, M. F. S. (2014). Comparison of Human Ventral Frontal Cortex Areas for Cognitive Control and Language with Areas in Monkey Frontal Cortex. *Neuron*, *81*(3), 700–713. https://doi.org/10.1016/j.neuron.2013.11.012

Newman, S. D., Just, M. A., Keller, T. A., Roth, J., & Carpenter, P. A. (2003). Differential effects of syntactic and semantic processing on the subregions of Broca’s area. *Cognitive Brain Research*, *16*(2), 297–307. https://doi.org/10.1016/S0926-6410(02)00285-9

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*, 156869. https://doi.org/10.1155/2011/156869

Ortells, J. J., Kiefer, M., Castillo, A., Megías, M., & Morillas, A. (2016). The semantic origin of unconscious priming: Behavioral and event-related potential evidence during category congruency priming from strongly and weakly related masked words. *Cognition*, *146*, 143–157. https://doi.org/10.1016/j.cognition.2015.09.012

Osterhaut, L., & Holcomb, P. J. (1992). Event-related brain potentials elicited by syntactic anomaly. *Journal of Memory & Language*, *31*, 785–806.

Pallier, C., Devauchelle, A.-D., & Dehaene, S. (2011). Cortical representation of the constituent structure of sentences. *Proceedings of the National Academy of Sciences*, *108*(6), 2522–2527. https://doi.org/10.1073/pnas.1018711108

Pinker, S., & Jackendoff, R. (2005). The faculty of language: What’s special about it? *Cognition*, *95*, 201–236. https://doi.org/10.1016/j.cognition.2004.08.004

Pulvermüller, F., & Shtyrov, Y. (2003). Automatic processing of grammar in the human brain as revealed by the mismatch negativity. *NeuroImage*.

https://doi.org/10.1016/S1053-8119(03)00261-1

Rabagliati, H., Robertson, A., & Carmel, D. (2018). The Importance of Awareness for Understanding Language. *Journal of Experimental Psychology: General*, *147*(2), 190–208. Retrieved from http://dx.doi.org/10.1037/xge0000348.supp

Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary Suppression of Visual Processing in an RSVP Task: An Attentional Blink? *Journal of Experimental Psychology: Human Perception and Performance*, *18*(3), 849–860.

Reingold, E. M., & Merikle, P. M. (1988). Using direct and indirect measures to study perception without awareness. *Perception & Psychophysics*, *44*, 563–575.

Reverberi, C., Görgen, K., & Haynes, J. D. (2012). Compositionality of rule representations in human prefrontal cortex. *Cerebral Cortex*, *22*(6), 1237–1246. https://doi.org/10.1093/cercor/bhr200

Ricker, T. J., & Sandry, J. (2018). The relationship between masking and short-term consolidation during recall from visual working memory. *Annals of the New York Academy of Sciences*, *1424*, 91–101. https://doi.org/10.1111/nyas.13641

Rilling, J. K. (2014). Comparative primate neuroimaging: Insights into human brain evolution. *Trends in Cognitive Sciences*, *18*(1), 46–55. https://doi.org/10.1016/j.tics.2013.09.013

Rodd, J. M., Davis, M. H., & Johnsrude, I. S. (2005). The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. *Cerebral Cortex*, *15*(8), 1261–1269. https://doi.org/10.1093/cercor/bhi009

Rohaut, B., Faugeras, F., Chausson, N., King, J. R., Karoui, I. El, Cohen, L., & Naccache, L. (2015). Probing ERP correlates of verbal semantic processing in patients with impaired consciousness. *Neuropsychologia*, *66*, 279–292. https://doi.org/10.1016/j.neuropsychologia.2014.10.014

Rohaut, B., & Naccache, L. (2018). What are the boundaries of unconscious semantic cognition? *European Journal of Neuroscience*, *47*(11), 1287–1288. https://doi.org/10.1111/ejn.13930

Salmelin, R. (2007). Clinical neurophysiology of language: The MEG approach. *Clinical Neurophysiology*, *118*(2), 237–254. https://doi.org/10.1016/j.clinph.2006.07.316

Schoffelen, J.-M., Hultén, A., Lam, N., Marquand, A. F., Uddén, J., & Hagoort, P. (2017). Frequency-specific directed interactions in the human brain network for language. *Proceedings of the National Academy of Sciences*, *114*(30), 8083–8088. https://doi.org/10.1073/pnas.1703155114

Scott, R. B., Samaha, J., Chrisley, R., & Dienes, Z. (2018). Prevailing theories of consciousness are challenged by novel cross-modal associations acquired between subliminal stimuli. *Cognition*, *175*, 169–185. https://doi.org/10.1016/j.cognition.2018.02.008

Shanks, D. R. (2017). Regressive research: The pitfalls of post hoc data selection in the study of unconscious mental processes. *Psychonomic Bulletin and Review*, *24*(3), 752–775. https://doi.org/10.3758/s13423-016-1170-y

Simons, J. S., & Spiers, H. J. (2003). Prefrontal and medial temporal lobe interactions in long-term memory. *Nature Reviews Neuroscience*, *4*(8), 637–648. https://doi.org/10.1038/nrn1178

Sklar, A. Y., Levy, N., Goldstein, A., Mandel, R., Maril, A., & Hassin, R. R. (2012). Reading and doing arithmetic nonconsciously. *Proceedings of the National Academy of Sciences*, *109*(48), 19614–19619. https://doi.org/10.1073/pnas.1211645109

Snijders, T. M., Vosse, T., Kempen, G., Van Berkum, J. J. A., Petersson, K. M., & Hagoort, P. (2009). Retrieval and unification of syntactic structure in sentence comprehension: An fMRI study using word-category ambiguity. *Cerebral Cortex*, *19*(7), 1493–1503. https://doi.org/10.1093/cercor/bhn187

Soto, D., & Silvanto, J. (2014). Reappraising the relationship between working memory and conscious awareness. *Trends in Cognitive Sciences*, *18*(10), 520–525. https://doi.org/10.1016/j.tics.2014.06.005

Spoormaker, V. I., Gleiser, P. M., & Czisch, M. (2012). Frontoparietal connectivity and hierarchical structure of the brain's functional network during sleep. *Frontiers in Neurology*, *3*, 1–10. https://doi.org/10.3389/fneur.2012.00080

Stein, T., Hebart, M., & Sterzer, P. (2011). Breaking continuous flash suppression: A measure of unconscious processing during interocular suppression? *Journal of Vision*, *11*(11), 315–315. https://doi.org/10.1167/11.11.315

Stein, T., Utz, V., & van Opstal, F. (2018). Unconscious semantic priming from pictures under backward masking and continuous flash suppression. *PsyArXiv [Preprint]*. Retrieved from https://doi.org/10.31234/osf.io/8sfep

Steppacher, I., Kaps, M., & Kissler, J. (2016). Against the odds: A case study of recovery from coma after devastating prognosis. *Annals of Clinical and Translational Neurology*, *3*(1), 61–65. https://doi.org/10.1002/acn3.269

Strauss, M., & Dehaene, S. (2019). Detection of arithmetic violations during sleep. *Sleep*, *42*(3), 1–12. https://doi.org/10.1093/sleep/zsy232

Stuellein, N., Radach, R. R., Jacobs, A. M., & Hofmann, M. J. (2016). No one way ticket from orthography to semantics in recognition memory: N400 and P200 effects of associations. *Brain Research*, *1639*, 88–98. https://doi.org/10.1016/j.brainres.2016.02.029

Tagliazucchi, E., von Wegner, F., Morzelewski, A., Brodbeck, V., Jahnke, K., & Laufs, H. (2013). Breakdown of long-range temporal dependence in default mode and attention networks during deep sleep. *Proceedings of the National Academy of Sciences*, *110*(38), 15419–15424. https://doi.org/10.1073/pnas.1312848110

Thompson-Schill, S. L., Bedny, M., & Goldberg, R. F. (2005). The frontal lobes and the regulation of mental activity. *Current Opinion in Neurobiology*, *15*(2), 219–224. https://doi.org/10.1016/j.conb.2005.03.006

Thompson, S. P., & Newport, E. L. (2007). Statistical Learning of Syntax: The Role of Transitional Probability. *Language Learning and Development*, *3*(1), 1–42. https://doi.org/10.1207/s15473341lld0301_1

Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, *381*(6582), 520–522. https://doi.org/10.1038/381520a0

Todd, A. R., Molden, D. C., Ham, J., & Vonk, R. (2011). The automatic and co-occurring activation of multiple social inferences. *Journal of Experimental Social Psychology*, *47*, 37–49. https://doi.org/10.1016/j.jesp.2010.08.006

Tononi, G., & Edelman, G. M. (1998). Consciousness and complexity. *Science*, *282*, 1846–1851. https://doi.org/10.1126/science.282.5395.1846

Tononi, G., & Koch, C. (2008). The neural correlates of consciousness: An update. *Annals of the New York Academy of Sciences*. https://doi.org/10.1196/annals.1440.004

Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, *8*(8), 1096–1101. https://doi.org/10.1038/nn1500

Turken, A. U., & Dronkers, N. F. (2011). The Neural Architecture of the Language Comprehension Network: Converging Evidence from Lesion and Connectivity Analyses. *Frontiers in System Neuroscience*, *5*, 1–20. https://doi.org/10.3389/fnsys.2011.00001

Tyler, L. K., Marslen-Wilson, W. D., Randall, B., Wright, P., Devereux, B. J., Zhuang, J., … Stamatakis, E. A. (2011). Left inferior frontal cortex and syntax: Function, structure and behaviour in patients with left hemisphere damage. *Brain*, *134*(2), 415–431. https://doi.org/10.1093/brain/awq369

Van den Bussche, E., Notebaert, K., & Reynvoet, B. (2009). Masked primes can be genuinely semantically processed. A picture prime study. *Experimental Psychology*, *56*(5), 295–300. https://doi.org/10.1027/1618-3169.56.5.295

Van den Bussche, E., Van den Noortgate, W., & Reynvoet, B. (2009). Mechanisms of Masked Priming: A Meta-Analysis. *Psychological Bulletin*, *135*(3), 452–477. https://doi.org/10.1037/a0015329

van Gaal, S., de Lange, F. P., & Cohen, M. X. (2012). The role of consciousness in cognitive control and decision making. *Frontiers in Human Neuroscience*, *6*(121), 1–15. https://doi.org/10.3389/fnhum.2012.00121

van Gaal, S., Naccache, L., Meuwese, J. D. I., van Loon, A. M., Leighton, A. H., Cohen, L., & Dehaene, S. (2014). Can the meaning of multiple words be integrated unconsciously? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1641), 20130212. https://doi.org/10.1098/rstb.2013.0212

van Gaal, S., Ridderinkhof, K. R., Scholte, H. S., & Lamme, V. A. F. (2010). Unconscious Activation of the Prefrontal No-Go Network. *Journal of Neuroscience*, *30*(11), 4143–4150. https://doi.org/10.1523/JNEUROSCI.2992-09.2010

Van Opstal, F., Reynvoet, B., & Verguts, T. (2005a). How to trigger elaborate processing? A comment on Kunde, Kiesel, and Hoffmann (2003). *Cognition*, *97*, 89–97. https://doi.org/10.1016/j.cognition.2004.12.011

Van Opstal, F., Reynvoet, B., & Verguts, T. (2005b). Unconscious semantic categorization and mask interactions: An elaborate response to Kunde et al. (2005). *Cognition*, *97*, 107–113. https://doi.org/10.1016/j.cognition.2005.04.005

Velmans, M. (1991). Is Human information processing conscious? *Behavioral and Brain Sciences*, *14*(4), 651–668.

Wang, L., Uhrig, L., Jarraya, B., & Dehaene, S. (2015). Representation of Numerical and Sequential Patterns in Macaque and Human Brains. *Current Biology*, *25*(15), 1966–1974. https://doi.org/10.1016/j.cub.2015.06.035

Wassenaar, M., & Hagoort, P. (2005). Word-category violations in patients with Broca's aphasia: An ERP study. *Brain and Language*, *92*(2), 117–137. https://doi.org/10.1016/j.bandl.2004.05.011

Willems, R. M., Özyürek, A., & Hagoort, P. (2007). When language meets action: The neural integration of gesture and speech. *Cerebral Cortex*, *17*(10), 2322–2333. https://doi.org/10.1093/cercor/bhl141

Willems, R. M., Özyürek, A., & Hagoort, P. (2008). Seeing and hearing meaning: ERP and fMRI evidence of word versus picture integration into a sentence context. *Journal of Cognitive Neuroscience*, *20*(7), 1235–1249. https://doi.org/10.1162/jocn.2008.20085

Xiang, H. D., Fonteijn, H. M., Norris, D. G., & Hagoort, P. (2010). Topographical functional connectivity pattern in the perisylvian language networks. *Cerebral*

Cortex, *20*(3), 549–560. https://doi.org/10.1093/cercor/bhp119

Yang, Y. H., Tien, Y. H., Yang, P. L., & Yeh, S. L. (2017). Role of consciousness in temporal integration of semantic information. *Cognitive, Affective and Behavioral Neuroscience*, *17*(5), 954–972. https://doi.org/10.3758/s13415-017-0525-9

Nederlandse samenvatting

De meeste levende wezens hebben een manier van communiceren. De menselijke communicatie is echter anders dan dat van welk ander levend wezen dan ook. Waarom? Terwijl de meeste dieren continu en zonder enkele inspanning communiceren, is menselijke communicatievaardigheid, die we taal noemen, virtueel oneindig in zijn uitdrukkingscapaciteit. Mensen zijn in staat om met hun woorden hele werelden te creeëren. Hoe dat komt? De vaardigheid van het menselijke brein om een eindig aantal woorden flexibel te combineren tot een oneindig aantal zinnen is een cruciale, nog steeds onbeantwoorde vraag.

Binnen de taalverwerking kan men het onderscheid maken tussen het verwerken van enkele woorden en hele zinnen. Aangezien het meeste neurowetenschappelijke onderzoek de laatste decennia zich heeft gefocust op het niveau van enkele woorden, is er weinig bekend over hoe de hersenen taal verwerken op zinsniveau. Gedurende deze these heb ik onderzocht welke hersenmechanismes ons in staat stellen om zin- en woordverwerking uit elkaar te trekken. Specifiek heb ik de voorspelling getoetst dat feedbackverwerking (top-downverwerking), waarschijnlijk vanaf de frontale naar de temporale gebieden, vereist is voor het verwerken van zinnen, maar niet voor het verwerken van enkele woorden. Ik heb visuele masking gebruikt als een middel om dit te onderzoeken. Visuele masking is een experimentele techniek die visueel gepresenteerde woorden "onzichtbaar" maakt, door ze kort te laten flitsen op het computerscherm, verborgen tussen andere visuele stimuli. Daarom zijn de participanten niet volledig bewust van dat ze woorden hebben gezien, ook al zijn hun hersenen aan deze blootgesteld. Voorgaand onderzoek naar visuele perceptie heeft laten zien dat masking feedbackverwerking verstoort, terwijl feedforwardverwerking (bottom-upverwerking) gespaard blijft. In deze these heb ik masking gebruikt om feedback te verstoren en heb ik onderzocht of, onder deze condities, zinsverwerking verstoord werd terwijl het verwerken van enkele woorden gespaard bleef.

Gedurende vier experimenten heb ik opnames gemaakt van het electroencephalografie (EEG) signaal terwijl participanten gemaskeerde zinnen en woorden zagen. Het is aangetoond dat gemaskeerd woorden neurale signaturen opwekken die vergelijkbaar zijn aan die van volledig zichtbare woorden, tenminste onder specifieke experimentele condities. Daarentegen is het controversieel of het mogelijk is om zinnen te encoderen onder verminderde bewustzijnsomstandigheden. In de studies die ik heb uitgevoerd, heb ik de neurale signatuur van gemaskeerde vs. volledig zichtbare zinnen en woorden vergeleken.

In hoofdstuk 2 en 3 heb ik me gericht op het semantische aspect van zinsverwerking, dat wil zeggen, het aspect gerelateerd aan het combineren van woordbetekenissen tot een zin. In hoofdstuk 2 heb ik gemaskeerde en ongemaskeerde verwerking van sequentieel gepresenteerde zinnen en woorden vergeleken. Aangezien ik gevonden had dat neurale signaturen van semantische verwerking in de gemaskeerde conditie van kortstondige aard waren, heb ik in hoofdstuk 3 gelijktijdig gepresenteerde zinnen en woorden vergeleken. In hoofdstuk 4 en 5 heb ik me gericht op het syntactische aspect van zinsverwerking, dat wil zeggen, het combineren van woorden tot een grammatical correct gevormde structuur. In hoofdstuk 4 heb ik taakgerelateerde effecten gevonden op zowel gemaskeerde als ongemaskeerde zins- en woordverwerking. Ik heb een follow-up experiment uitgevoerd, gerapporteerd in hoofdstuk 5, om deze taakgerelateerde effecten verder te onderzoeken.

In het algemeen heb ik gevonden dat masking zinsverwerking, maar niet woordverwerking, verstoort. Over de vier experimenten heen gezien, heb ik duidelijke neurale signaturen van linguistische verwerking waargenomen. Als woorden daarentegen waren gemaskeerd waren deze signaturen alleen aanwezig voor enkele woorden (en slechts onder bepaalde experimentele condities), maar niet voor zinnen. Dit suggereert dat taalcombinatorische processen, zowel op het semantische als het syntactische niveau, volledig bewustzijn vereisen, terwijl woordverwerking ook bij verminderde bewustzijnsniveaus kan plaatsvinden. Samengenomen suggereren deze resultaten dat feedbackverwerking, waarbij waarschijnlijk frontale en temporele gebieden betrokken zijn, vereist zijn voor zinsverwerking, maar niet voor het verwerken van enkele woorden. Dit impliceert dat verschillende hersenmechanismes betrokken zijn bij zins- en woordverwerking, hetgeen nieuwe inzichten verschaft voor huidige debatten over de specifieke rollen van verschillende hersenmechanismen in het gedistribueerde taalnetwerk.

English summary

Most living creatures have a code of communication. Still, human communication code uniquely differs from that of any other living entity. Why? While most animals communicate continuously and effortlessly, human communication faculty, which we call language, is the only faculty that is virtually infinite in its capacity of expression. Humans are able to create entire worlds with words. How come? The ability of the human brain to flexibly combine a finite amount of words into an infinite set of sentences is a crucial, still unanswered issue.

Within language processing, one can distinguish between single word and sentence (combinatorial) processing. As most neuroscience research in the last decades focused on the single word level, little is known on how the brain processes language at the sentence level. In the course of my thesis, I investigated which brain mechanisms allow us to disentangle sentence and single word processing. In particular, I tested the prediction that feedback (top-down) processing, most likely from frontal to temporal areas, is required for sentence processing, but not for single word processing. I employed visual masking as a tool to investigate this issue. Visual masking is an experimental technique that makes visually presented words “invisible” by briefly flashing them on the computer screen, hidden among other visual stimuli. Therefore, participants are not fully aware of seeing the words, although their brain is exposed to them. Previous research on visual perception showed that masking disrupts feedback processing, while preserving feedforward (bottom-up) processing. In this thesis, I employed masking to disrupt feedback and investigated whether, under these conditions, sentence processing was impaired while single word processing was spared.

Across four experiments, I recorded the electroencephalography (EEG) signal while participants saw masked sentences and single words. It has been shown that masked single words may trigger neural signatures that are similar to those of fully visible words, at least under certain experimental conditions. On the contrary, the possibility of sentence encoding under reduced levels of awareness is controversial. In the studies I performed, I compared the neural signatures of masked vs. fully visible sentences and single words.

In Chapter 2 and 3, I focused on the semantic aspect of sentence processing, that is the aspect related to the combination of word meanings into a sentence. In Chapter 2, I compared masked and unmasked processing of sequentially presented sentences and single words. Since I found that the neural signatures of semantic processing in the masked condition were short-lived, in Chapter 3 I compared simultaneously presented sentences and single words. In Chapter 4 and 5, I focused on the syntactic aspect of sentence processing, that is the combination of words into a grammatically well-formed structure. In Chapter 4, I found task-related effects on both masked and unmasked sentence and single word processing. I conducted a follow-up experiment, reported in Chapter 5, in order to further investigate these task-related effects.

Overall, I found that masking disrupts sentence processing, but not single word processing. Across the four experiments, I observed clear neural signatures of linguistic processing for both unmasked sentences and single words. On the contrary, when words were masked these signatures were only present for single words (and only until certain experimental conditions), but not for sentences. This suggests that language combinatorial processes, both at the semantic and the syntactic level, may require full awareness, whereas single word processing may occur under reduced levels of awareness. Taken together, these results suggest that feedback processing, likely involving frontal and temporal areas, is required for sentence processing, but not for single word processing. This implies that distinct brain mechanisms may be involved in sentence and single word processing, adding new insights to ongoing debates about the specific roles of different brain mechanisms in a distributed language network.

Curriculum Vitae

Valeria Mongelli was born on September 7th 1990 in Bari, Italy. In 2008, after passing the entrance exam at the Scuola Normale Superiore, she moved to Pisa to study Philosophy. In 2010, Valeria won a study fellowship at the Ecole Normale Supérieure (ENS) in Lyon, and spent nine months there to study philosophy of mind and learn French. In 2011, she won the ENS Master fellowship (Sélection Internationale). Therefore, after receiving her Bachelor in Pisa, she moved again to Lyon to start a Linguistics Master that she completed in 2013. In 2012, during her second year of Master, she also started a Master in Cognitive Science in Paris (ENS/Ecole des Hautes Etudes en Sciences Sociales/Paris 5). In 2013, Valeria did a research internship at the Brain and Spine Institute in Paris, where she scanned musicians' brains and discovered the fascinating world of brain imaging under the supervision of Laurent Cohen. After getting her second Master, she left Europe and crossed South America with her backpack and her camera. In 2015, Valeria joined the Neurobiology of Language group at the Max Planck Institute for Psycholinguistics in Nijmegen, where she started a PhD on the interactions between language and conscious awareness under the supervision of Peter Hagoort and Simon van Gaal (University of Amsterdam). In 2017, she won the poster award at ASSC (Association for the Scientific Study of Consciousness) conference in Beijing and moved to Simon's Conscious Lab at the University of Amsterdam. In parallel to her PhD, Valeria regularly works as a freelance photographer. In 2018-2019, she worked as a journalist and photojournalist for two online, Amsterdam-based newspapers (The Amsterdammer and 31mag.nl). Her long-term photodocumentary project *Free to be*, a reportage of Amsterdam squats, has been exhibited in multiple venues in Amsterdam. Currently, Valeria is working at her personal photography and writing projects, planning a trip to South-East Asia and trying to understand her place in the world.

Publications

Mongelli, V., Meijs, E.L., van Gaal, S., & Hagoort, P. (2019). No language unification without neural feedback : How awareness affects sentence processing. *NeuroImage, 202*, 1-12.

Mongelli, V., Dehaene, S., Vinckier, F., Peretz, I., Bartolomeo, P., & Cohen, L. (2017). Music and words in the visual cortex : The impact of musical expertise. *Cortex, 86*, 260-274.

Bouhali, F., **Mongelli, V**., & Cohen, L. (2017). Musical literacy shifts asymmetries in the ventral visual cortex. *NeuroImage, 156*, 445-455.

Jayez, J., **Mongelli, V**., Reboul, A., & Van der Henst, J. (2015). Weak and strong triggers. In F. Schwarz (Ed.), *Experimental Perspectives on Presuppositions* (173-194), Berlin: Springer.

Jayez, J., & **Mongelli, V**. (2013). How hard are hard triggers? *Actes de Sinn und Bedeutung, 17*, 307-324.

Submitted:

Mongelli, V., Meijs, E.L., Hagoort, P., & van Gaal, S. The role of awareness and task set in syntactic unification.

Bouhali, F., **Mongelli, V**., Thiebaut de Schotten, M. & Cohen, L. Reading music and words: the anatomical connectivity of musicians' visual cortex.

In preparation:

Mongelli, V., Meijs, E.L., Hagoort, P. & van Gaal, S. The role of prime novelty and task set in masked semantic priming.

Acknowledgements

I am a lucky girl.

I am not an easy person to work with. First of all, I am not patient. I am exigent. I am not very diplomatic. I do not have much respect for the authority. I am not a morning person.

Despite all this, in my journey through the academic world I had the chance to work with great people. Peter, thanks for opening me the doors of MPI, for letting me free (both geographically and intellectually), for always setting the bar high and, last but not least, for showing me that one can still be passionate about research after years of experience. Simon, in these four years you have seen me in all possible moods: depressed and enthusiastic, relieved and desperate… I hope that the good moments counterbalance the bad ones. For me they do. Thanks for hosting me in your group, for never losing your temper (it should not have been always easy), for always trying to downplay issues. Thanks for being there whenever I needed.

Erik, you are an extremely talented programmer, a wonderful teacher and a truly kind person. If I learned some Fieldtrip, that is only thanks to you. Matlab has always been in my top ranking of painful things, and you managed to explain it to me in a way that I understood. Thank you.

Thanks to both the NBL and the Conscious Brain Lab for creating such a vibrant and challenging intellectual environment.

Thanks to Camilla, Nutsa, Birgit, Iris and Eva for helping to collect EEG data from more than 200 participants. I can't even quantify how many hours of work that took. Thanks for making such a fundamental contribution to this thesis.

I am a lucky girl because I had amazing teachers since I was very young.

Pino Di Florio teaches Frege to sixteen-year old teenagers. Seriously. In a country where public education has been systematically destroyed for decades, and schools literally fall apart. If it wasn't for you, probably I would have never started wondering how our mind produces those magical entities that we call words. Thank you.

When I was eighteen, I had the chance of studying with one of the greatest living historians in the world. Carlo Ginzburg is an astonishing example of pure love for research. I remember his lessons as one of the most mind-blowing intellectual experiences I have ever had. In a recent interview, talking about his last study, he admitted being quite annoyed as he found exactly what he was looking for. In science, we often stop searching as soon as we validate our initial hypothesis. Maybe empirical research should learn something from this approach in humanities. Thank you, forever thank you for your clarity of mind and intellectual honesty.

Thanks to Laurent Cohen for teaching me the bases of neuroimaging from scratch. You prepared me well to this PhD journey (except for its frustrating part).

I am a lucky girl because, despite moving to five different cities in the last ten years, I met many great colleagues and true friends.

Thanks to Marvin and René, my first office mates. When I arrived in Nijmegen in September 2015, I just came back from a long, life-changing trip to Latin America. I left Paris, which I loved, and my previous life there. Moving to the Netherlands was both a cultural and an emotional shock. No one more than you witnessed it in the daily routine. Thanks for being there, both during those hard times and later.

Yingying, thanks for being the sweetest office neighbor. Markus, thanks for being such a smart and, at the same time, humble, curious and pleasant person. Limor, thanks for your wonderful and relentless energy. Lara, thanks for the coffees, the beers, the chats, the laughs and the support.

Thanks to my Nijmegen Italian crew. Paolo and Ari, you brought a piece of home in this Northern, cold land. Thanks for your always heartwarming hospitality. Cecilia, you will always be my favorite party woman, even if we do not live in the same country anymore. David, you also helped me quite a lot during my coding crises. Thanks man! I will never forget when, in a freezing morning of February, we got lost in the Nijmegen countryside after a party and I almost died of hypothermia (lol).

Thanks to Timo, my first office mate in Amsterdam and favorite party man. Thanks for being the amazing and crazy person you are. Looking forward to more party adventures together.

Thanks to my current UvA office mates: Daniel (my other favorite party man), Annabeth, Joost (special thanks for all the Dutch translations!), João.

Thanks to the whole book club crew: Giacomo, Johnny, Jonas, Ceren, Damiano, Joris, Merel. Diego, thanks for throwing up on my friends' carpets, importing Apulian homemade grappa in fuel jugs, and for the unforgettable Umpa-Lumpa party. Maria Chiara, thanks for the chats at UvA, the nights out, your omnipresent smile. Thanks to Matt and Hayley, my favorite jazz concert buddies. Ruben, thanks for all the good vibes. Mario, thanks for being my friend since 2009. It is great to have you close by again. And I am happy you are finally in your teenager phase (mine never ended). Thanks to Abdo, my third favorite party man (I realize I have too many). Erica, thanks for the wine evenings at De Pijp, the complaining vocal messages on Monday mornings, the laughs and the movie nights. Stefano, thank you so much for your precious graphic designer help. Thanks to Anderson, my favorite defense photographer.

Thanks to my wonderful paranymphs. Damiano, thanks for being such a generous friend, a true support, and a constant wave of positivity. Nico, thanks for being my partner in crime in discovering the underground side of Amsterdam, for our chats mixing Spanish and English, for patiently listening to my complaints in the hard days. You were one of the few saying that something I cooked was good (not sure it was true though). Sara, thanks for being my personal rainbow at MPI, for both the ups and the downs of our friendship, for reminding me to be proud of myself. I love you guys.

Falling in love with Amsterdam was like falling in love with someone that is completely different from me. It was strong, and unexpected. Thanks Amsterdam for being such a great and diverse place. And thanks to those who made possible my photography adventures through Amsterdam squats. It was like travelling from my doorstep.

I am a lucky girl because I am a nomad, but I have friendships that are incredibly resistant to time and distance.

Francesco, thanks for being my adventure companion in Bari, Paris, the Netherlands and hopefully many forthcoming places.

Irene, thanks for being the strong and wonderful woman you are. It is a privilege to be your friend. To the wine we will always try to pour from closed bottles.

To my life-long friends: Martina, Dario, Ale. I do not need to add why.

Silvia, thanks for being at my side since I am three.

I am a lucky girl, because I have always had successful and peaceful relationships. No, this is not true. Still, there are a couple ones I feel to save from the ruins.

To Edo, who saw more than half of this thesis growing. Thanks for the time we spent together, until we managed to make it work.

To Pierpaolo. Once, talking about this thesis, you told me to make something beautiful out of doubt. Thinking of your words, I often feel as if you thought all my best thoughts beforehand. Doubts are still here. I am not sure it is a good thing. For sure it does not make things easier. However, without doubt there is no question, and without question there is no research. I am still trying to make something beautiful out of it.

I am a lucky girl, because my family is an anchor in the ocean of my flowing life.

Nico, thanks for being there whenever I need, for being the older brother sometimes, and for showing me that one can achieve big goals while staying chill. I am so proud of you.

Mom and dad, thanks for showing me every day the importance of love beyond differences. Mamma e papà, grazie per mostrarmi ogni giorno l'importanza dell'amore al di là delle differenze.

Thanks Dona, my third grandmother. Grazie a Dona, la mia terza nonna.

I am a lucky girl, because I waited until last year to watch the departure of one of my most beloved ones. Thanks grandma. In a place, Southern Italy, where women's bodies and thoughts are often property of someone else, you showed me the importance of doing what you want and choosing what you love. Thanks for proving me that if you want to, you can end up riding elephants in Bangkok, even if you are an Apulian housewife in the ‘60s. Thanks for being a free woman until your last day.

Doing this PhD was like holding my breath for four years.

I started studying the brain because I was looking for true things. From the highness of philosophical concepts I went down, cutting an idea into small pieces and trying to prove at least one of them. I dug deeper and deeper, but just found smaller pieces. I was looking for truth, and I found matrices of numbers instead. That was tough. Still, years of frustration did not manage to completely delete what I consider as the maximum pleasure of research: those rare, brief moments in which thoughts organize by themselves, and words seem to shape the world. It is just an illusion, of course. But the beauty of intellectual work is all there. I am still not sure what to make out of it. However, empirical research taught me to accept a bit more that reality will never be as I have in mind. And maybe it is more fun this way.

Hay vidas ordenadas que se merecen su línea de tiempo,
esa escalerita donde los hechos se encadenan seguros.
Pero hay existencias más lúdicas.
“There are tidy lives that deserve a timeline,
a small ladder on which facts safely follow each other.
Then there are more playful lives.”

Miguel Rep, from the preface to Julio Cortázar’s biography

MPI Series in Psycholinguistics

1. The electrophysiology of speaking: Investigations on the time course of semantic, syntactic, and phonological processing. *Miranda van Turennout*
2. The role of the syllable in speech production: Evidence from lexical statistics, metalinguistics, masked priming, and electromagnetic midsagittal articulography. *Niels O. Schiller*
3. Lexical access in the production of ellipsis and pronouns. *Bernadette M. Schmitt*
4. The open-/closed-class distinction in spoken-word recognition. *Alette Haveman*
5. The acquisition of phonetic categories in young infants: A self-organising artificial neural network approach. *Kay Behnke*
6. Gesture and speech production. *Jan-Peter de Ruiter*
7. Comparative intonational phonology: English and German. *Esther Grabe*
8. Finiteness in adult and child German. *Ingeborg Lasser*
9. Language input for word discovery. *Joost van de Weijer*
10. Inherent complement verbs revisited: Towards an understanding of argument structure in Ewe. *James Essegbey*
11. Producing past and plural inflections. *Dirk Janssen*
12. Valence and transitivity in Saliba: An Oceanic language of Papua New Guinea. *Anna Margetts*
13. From speech to words. *Arie van der Lugt*
14. Simple and complex verbs in Jaminjung: A study of event categorisation in an Australian language. *Eva Schultze-Berndt*
15. Interpreting indefinites: An experimental study of children's language comprehension. *Irene Krämer*
16. Language-specific listening: The case of phonetic sequences. *Andrea Weber*
17. Moving eyes and naming objects. *Femke van der Meulen*
18. Analogy in morphology: The selection of linking elements in Dutch compounds. *Andrea Krott*
19. Morphology in speech comprehension. *Kerstin Mauth*
20. Morphological families in the mental lexicon. *Nivja H. de Jong*
21. Fixed expressions and the production of idioms. *Simone A. Sprenger*
22. The grammatical coding of postural semantics in Goemai (a West Chadic language of Nigeria). *Birgit Hellwig*

23. Paradigmatic structures in morphological processing: Computational and cross-linguistic experimental studies. *Fermín Moscoso del Prado Martín*
24. Contextual influences on spoken-word processing: An electrophysiological approach. *Daniëlle van den Brink*
25. Perceptual relevance of prevoicing in Dutch. *Petra M. van Alphen*
26. Syllables in speech production: Effects of syllable preparation and syllable frequency. *Joana Cholin*
27. Producing complex spoken numerals for time and space. *Marjolein Meeuwissen*
28. Morphology in auditory lexical processing: Sensitivity to fine phonetic detail and insensitivity to suffix reduction. *Rachèl J. J. K. Kemps*
29. At the same time...: The expression of simultaneity in learner varieties. *Barbara Schmiedtová*
30. A grammar of Jalonke argument structure. *Friederike Lüpke*
31. Agrammatic comprehension: An electrophysiological approach. *Marlies Wassenaar*
32. The structure and use of shape-based noun classes in Miraña (North West Amazon). *Frank Seifart*
33. Prosodically-conditioned detail in the recognition of spoken words. *Anne Pier Salverda*
34. Phonetic and lexical processing in a second language. *Mirjam Broersma*
35. Retrieving semantic and syntactic word properties. *Oliver Müller*
36. Lexically-guided perceptual learning in speech processing. *Frank Eisner*
37. Sensitivity to detailed acoustic information in word recognition. *Keren B. Shatzman*
38. The relationship between spoken word production and comprehension. *Rebecca Özdemir*
39. Disfluency: Interrupting speech and gesture. *Mandana Seyfeddinipur*
40. The acquisition of phonological structure: Distinguishing contrastive from non-contrastive variation. *Christiane Dietrich*
41. Cognitive cladistics and the relativity of spatial cognition. *Daniel B.M. Haun*
42. The acquisition of auditory categories. *Martijn Goudbeek*
43. Affix reduction in spoken Dutch. *Mark Pluymaekers*
44. Continuous-speech segmentation at the beginning of language acquisition: Electrophysiological evidence. *Valesca Kooijman*
45. Space and iconicity in German Sign Language (DGS). *Pamela Perniss*

46. On the production of morphologically complex words with special attention to effects of frequency. *Heidrun Bien*
47. Crosslinguistic influence in first and second languages: Convergence in speech and gesture. *Amanda Brown*
48. The acquisition of verb compounding in Mandarin Chinese. *Jidong Chen*
49. Phoneme inventories and patterns of speech sound perception. *Anita Wagner*
50. Lexical processing of morphologically complex words: An information-theoretical perspective. *Victor Kuperman*
51. A grammar of Savosavo, a Papuan language of the Solomon Islands. *Claudia Wegener*
52. Prosodic structure in speech production and perception. *Claudia Kuzla*
53. The acquisition of finiteness by Turkish learners of German and Turkish learners of French: Investigating knowledge of forms and functions in production and comprehension. *Sarah Schimke*
54. Studies on intonation and information structure in child and adult German. *Laura de Ruiter*
55. Processing the fine temporal structure of spoken words. *Eva Reinisch*
56. Semantics and (ir)regular inflection in morphological processing. *Wieke Tabak*
57. Processing strongly reduced forms in casual speech. *Susanne Brouwer*
58. Ambiguous pronoun resolution in L1 and L2 German and Dutch. *Miriam Ellert*
59. Lexical interactions in non-native speech comprehension: Evidence from electro-encephalography, eye-tracking, and functional magnetic resonance imaging. *Ian FitzPatrick*
60. Processing casual speech in native and non-native language. *Annelie Tuinman*
61. *Split intransitivity in Rotokas, a Papuan language of Bougainville. Stuart Robinson*
62. Evidentiality and intersubjectivity in Yurakaré: An interactional account. *Sonja Gipper*
63. The influence of information structure on language comprehension: A neurocognitive perspective. *Lin Wang*
64. The meaning and use of ideophones in Siwu. *Mark Dingemanse*
65. The role of acoustic detail and context in the comprehension of reduced pronunciation variants. *Marco van de Ven*
66. Speech reduction in spontaneous French and Spanish. *Francisco Torreira*

67. The relevance of early word recognition: Insights from the infant brain. *Caroline Junge*
68. Adjusting to different speakers: Extrinsic normalization in vowel perception. *Matthias J. Sjerps*
69. Structuring language. Contributions to the neurocognition of syntax. *Katrien R. Segaert*
70. Infants' appreciation of others' mental states in prelinguistic communication: A second person approach to mindreading. *Birgit Knudsen*
71. Gaze behavior in face-to-face interaction. *Federico Rossano*
72. Sign-spatiality in Kata Kolok: how a village sign language of Bali inscribes its signing space**.** *Conny de Vos*
73. Who is talking? Behavioural and neural evidence for norm-based coding in voice identity learning. *Attila Andics*
74. Lexical processing of foreign-accented speech: Rapid and flexible adaptation. *Marijt Witteman*
75. The use of deictic versus representational gestures in infancy. *Daniel Puccini*
76. Territories of knowledge in Japanese conversation. *Kaoru Hayano*
77. Family and neighbourhood relations in the mental lexicon: A cross-language perspective. *Kimberley Mulder*
78. Contributions of executive control to individual differences in word production. *Zeshu Shao*
79. Hearing speech and seeing speech: Perceptual adjustments in auditory-visual processing. *Patrick van der Zande*
80. High pitches and thick voices: The role of language in space-pitch associations. *Sarah Dolscheid*
81. Seeing what's next: Processing and anticipating language referring to objects. *Joost Rommers*
82. Mental representation and processing of reduced words in casual speech. *Iris Hanique*
83. The many ways listeners adapt to reductions in casual speech. *Katja Poellmann*
84. Contrasting opposite polarity in Germanic and Romance languages: Verum Focus and affirmative particles in native speakers and advanced L2 learners. *Giuseppina Turco*
85. Morphological processing in younger and older people: Evidence for flexible dual-route access. *Jana Reifegerste*

86. Semantic and syntactic constraints on the production of subject-verb agreement. *Alma Veenstra*
87. The acquisition of morphophonological alternations across languages. *Helen Buckler*
88. The evolutionary dynamics of motion event encoding. *Annemarie Verkerk*
89. Rediscovering a forgotten language. *Jiyoun Choi*
90. The road to native listening: Language-general perception, language-specific input. *Sho Tsuji*
91. Infants'understanding of communication as participants and observers. *Gudmundur Bjarki Thorgrímsson*
92. Information structure in Avatime. *Saskia van Putten*
93. Switch reference in Whitesands. *Jeremy Hammond*
94. Machine learning for gesture recognition from videos. *Binyam Gebrekidan Gebre*
95. Acquisition of spatial language by signing and speaking children: a comparison of Turkish sign language (TID) and Turkish. *Beyza Sümer*
96. An ear for pitch: on the effects of experience and aptitude in processing pitch in language and music. *Salomi Savvatia Asaridou*
97. Incrementality and Flexibility in Sentence Production. *Maartje van de Velde*
98. Social learning dynamics in chimpanzees: Reflections on (nonhuman) animal culture. *Edwin van Leeuwen*
99. The request system in Italian interaction. *Giovanni Rossi*
100. Timing turns in conversation: A temporal preparation account. *Lilla Magyari*
101. Assessing birth language memory in young adoptees**.** *Wencui Zhou*
102. A social and neurobiological approach to pointing in speech and gesture. *David Peeters*
103. Investigating the genetic basis of reading and language skills. *Alessandro Gialluisi*
104. Conversation Electrified: The Electrophysiology of Spoken Speech Act Recognition***.*** *Rósa Signý Gisladottir*
105. Modelling Multimodal Language Processing. *Alastair Smith*
106. Predicting language in different contexts: The nature and limits of mechanisms in anticipatory language processing. *Florian Hintz*
107. Situational variation in non-native communication. *Huib Kouwenhoven*
108. Sustained attention in language production. *Suzanne Jongman*

109. Acoustic reduction in spoken-word processing: Distributional, syntactic, morphosyntatic, and orthographic effects. *Malte Viebahn*
110. Nativeness, dominance, and the flexibility of listening to spoken language. *Laurence Bruggeman*
111. Semantic specificity of perception verbs in Maniq. *Ewelina Wnuk*
112. On the identification of FOXP2 gene enhancers and their role in brain development. *Martin Becker*
113. Events in language and thought: The case of serial verb constructions in Avatime. *Rebecca Defina*
114. Deciphering common and rare genetic effects on reading ability. *Amaia Carrión Castillo*
115. Music and language comprehension in the brain. *Richard Kunert*
116. Comprehending Comprehension: Insights from neuronal oscillations on the neuronal basis of language**.** *Nietzsche H.L. Lam*
117. The biology of variation in anatomical brain asymmetries. *Tulio Guadalupe*
118. Language processing in a conversation context. *Lotte Schoot*
119. Achieving mutual understanding in Argentine Sign Language. *Elizabeth Manrique*
120. Talking Sense: the behavioural and neural correlates of sound symbolism. *Gwilym Lockwood*
121. Getting under your skin: The role of perspective and simulation of experience in narrative comprehension. *Franziska Hartung*
122. Sensorimotor experience in speech perception. *Will Schuerman*
123. Explorations of beta-band neural oscillations during language comprehension: Sentence processing and beyond. *Ashley Lewis*
124. Influences on the magnitude of syntactic priming. *Evelien Heyselaar*
125. Lapse organization in interaction. *Elliott Hoey*
126. The processing of reduced word pronunciation variants by natives and foreign language learners: Evidence from French casual speech. *Sophie Brand*
127. The neighbors will tell you what to expect: Effects of aging and predictability on language processing. *Cornelia Moers*
128. The role of voice and word order in incremental sentence processing. *Sebastian Sauppe*
129. Learning from the (un)expected: Age and individual differences in statistical learning and perceptual learning in speech. *Thordis Neger*

130. Mental representations of Dutch regular morphologically complex neologisms. *Laura de Vaan*
131. Speech production, perception, and input of simultaneous bilingual preschoolers: Evidence from voice onset time. *Antje Stoehr*
132. A holistic approach to understanding pre-history. *Vishnupriya Kolipakam*
133. Characterization of transcription factors in monogenic disorders of speech and language. *Sara Busquets Estruch*
134. Indirect request comprehension in different contexts. *Johanne Tromp*
135. Envisioning Language - An Exploration of Perceptual Processes in Language Comprehension. *Markus Ostarek*
136. Listening for the WHAT and the HOW: Older adults' processing of semantic and affective information in speech. *Juliane Kirsch*
137. Let the agents do the talking: on the influence of vocal tract anatomy on speech during ontogeny and glossogeny. *Rick Janssen*
138. Age and hearing loss effects on speech processing. *Xaver Koch*
139. Vocabulary knowledge and learning: Individual differences in adult native speakers. *Nina Mainz*
140. The face in face-to-face communication: Signals of understanding and non-understanding. *Paul Hömke*
141. Person reference and interaction in Umpila/Kuuku Ya'u narrative. *Clair Hill*
142. Beyond the language given: The neurobiological infrastructure for pragmatic inferencing. *Jana Bašnáková*
143. From Kawapanan to Shawi: Topics in language variation and change. *Luis Miguel Rojas-Berscia*
144. On the oscillatory dynamics underlying speech-gesture integration in clear and adverse listening conditions. *Linda Drijvers*
145. Understanding temporal overlap between production and comprehension. *Amie Fairs*
146. The role of exemplars in speech comprehension. *Annika Nijveld*
147. A network of interacting proteins disrupted in language-related disorders. *Elliot Sollis*
148. Fast speech can sound slow: Effects of contextual speech rate on word recognition. *Merel Maslowski*
149. Reason-giving in everyday activities. *Julija Baranova*
150. Speech planning in dialogue - Psycholinguistic studies of the timing of turn taking. *Mathias Barthel*

151. The role of neural feedback in language unification: How awareness affects combinatorial processing. *Valeria Mongelli*