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**Neural Correlates
of Language Learning
in Adults**



Neural correlates of language learning in adults

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*To my favorite language learners
Amanda and Antonella.*

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Acknowledgements

First, I would like to acknowledge volunteer participants who made the studies in this thesis possible. The studies were long and required several measurement sessions and often involved tedious training sessions; this has entailed both patience and dedication of the participants for which I'm most grateful.

I would equally like to thank my two supervisors Academy Professor Riitta Salmelin and professor Matti Laine. Riitta, your door has always been open and I have been able to seek advice and guidance at every step of the research. Your knowledge of the field never stops to impress me and I am honored and privileged to have been given the opportunity work with you and to befriend you. 'Thank you' hardly seems adequate to express the gratefulness I feel to you. Matti, you introduced me to psycholinguistics and have pushed me forward in the scientific field ever since my undergraduate studies. I admire both your scientific knowledge and your leadership talents, and I'm deeply indebted to you for enabling me to find my life passion; scientific research.

This work was carried out in the Brain Research Unit and in the Advance Magnetic Imaging Center of the Low Temperature Laboratory at the Aalto University. I am thankful for the opportunity to work in such a distinguished laboratory equipped with both talented people and resources for demanding scientific projects. The head of the laboratory professor Mikko Paalanen and the head of the Brain Research Unit, Academy Professor and Academician Riitta Hari deserve my sincere thanks for creating such an inspiring environment and for all personal support given to me during my time here. I am also thankful to the support personnel and secretaries in the laboratory.

In addition, I would like to thank everyone at the Department of Psychology and Logopedics at Åbo Akademi University. I would especially like to mention Dr Petra Grönholm for the practical help and encouragement, Susanne Maikola for all assistance and friendly reception and Professors Pekka Santtila and Kenneth Sandnabba for their pleasant co-operation while they have been heading the department.

I am sincerely grateful to my co-authors for all their contributions. Warm thank to Dr Minna Vihla, for teaching me how to measure and analyze MEG data and for being such a friendly and happy person. A very special thank you to Hannu Laaksonen for being a loyal friend, but also for all the deep scientific discussions we have had over the years. I am also extremely thankful to Dr Mia Liljeström, with whom I share both professional and private joys and sorrows; mostly joys. Thank you Mia, you cheer up my days! Working with Leena Karvonen and Anni Simula has been immensely fun, and you have also become valued friends to me. Thank you also for your remarkable patience with all my shortcomings when it comes to being a coherent well-organized instructor. Dr Lauri Parkkonen and Dr Minna Lehtonen are thanked for being such knowledgeable and inspiring persons, within their respective fields, and for being friends that one can count on!

I wish to express my gratitude to professor Elisabeth 'Lili' Service for all your valuable input both as a co-author and as a member of my follow-up group together

with professor Jan-Ola Östman. I have received not only valuable scientific support but also a personal mentorship from both of you. I am also grateful to Dr Jeong-Young Kim for her invaluable linguistic help in the study using Korean stimuli.

Warm hugs to all my past and present friends and colleagues at the Low Temperature Laboratory; Dr Topi Tanskanen, Dr Miiu Kujala, Dr Jan Kujala, Dr Tiina Parviainen, Dr Gina Caetano, Kaisa Hytönen, Liisa Helle, Maarit Aro, Dr Päivi Sivonen, Dr Hanna Renvall, Dr Clair Stevenson, Dr Paolo Belardinelli, Dr Silvia Aggujaro, Antti Jalava, Timo Saarinen, Henna Roikola, Paulina Ojala, Elli Vuokko, Tuomas Hirvonen, Linda Henrikson, Dr Ville Renvall, Lotta Hirvenkari, Anne Mandel, Pavan Ramkumar, Kritiina Roiha, Siina Pamilo, Dr Mika Seppä, Satu Lamminmäki, Dr Catherine Nangini, Dr Sebastian Pannasch, Dr Yevhen Hkuschuk among many others. To my close friends Dr Johanna Vartiainen, Dr Sanna Malinen and Dr Linda Stenbacka I want to express a special thank you; Johanna your optimism and life wisdom is an example to us all; Sanna and Linda you rock the world! In addition, I would also like to acknowledge Docent Päivi Helenius for all the advice, both personal and professional, that you have given me over the years. I am also grateful to all the persons who proof read or commented on the thesis manuscript; Dr Joann von Weissenberg, Dr Mia Liljeström, Dr Lauri Parkkonen and Aapo Lankinen.

On a very personal level I'm truly grateful to my parents May and Ralf Hultén as they have taught me to value knowledge and critical thinking. A big hug goes to my brother Kim Hultén and his precious family for their support over the years. My wonderful friends outside the work sphere have also shown to be worth their weight in gold. My beloved friend Miti von Weissenberg has shown me support and friendship beyond compare; despite being on opposite continents, skype connections have enabled moral support and encouragement from her that has pushed me through the inevitable setbacks that goes with the PhD work. The scientific conversations I have with my partner Aapo Lankinen truly spice up my evenings and have often helped me structure my thoughts. I am also immensely thankful for all the love and support I have received from you.

Finally, I wish to thank the Finnish Graduate School for Neuroscience and for the financial support provided by the Academy of Finland, the Finnish Cultural Foundation and Stiftelsen för Åbo Akademi.

Annika Hultén

List of original publications

- I. Liljeström, M., Hultén, A., Parkkonen, L., Salmelin, R. (2009) Comparing MEG and fMRI views to naming actions and objects. *Human Brain Mapping*, 30, 1845-1856
- II. Hultén, A., Vihla, M., Laine, M., Salmelin, R. (2009) Accessing newly learned names and meanings in the native language. *Human Brain Mapping*, 30, 976-89
- III. Hultén, A., Laaksonen, H., Vihla, M., Laine, M., Salmelin, R. (2010) Modulation of brain activity after learning predicts long-term memory for words. *Journal of Neuroscience* 30, 15160-15164
- IV. Hultén, A., Karvonen, L., Laine, M., Salmelin, R. (submitted) Sentence-level speech production with newly learned grammar and vocabulary.
- V. Simula*, A., Hultén*, A., Karvonen, L., Kim, J.-Y., Service, E., Salmelin, R. (submitted) Phonological learning in adults in a familiar and an unfamiliar phonological system.
*shared first authorship

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Author's contribution

The five Studies in the thesis are co-authored and a result of team work. All authors have participated in the planning and reporting. In Studies II-IV, I was the principal author, and had the main responsibility for the experiments. In these studies I collected the data and carried out the data analysis. In Study V, A.S. and I have shared first authorship, with equal contribution to all work stages. In Study I, I participated in collection and analysis of the MEG data and writing of the manuscript.

Swedish summary—Svensk sammanfattning

Människans språkförmåga utvecklas hela livet. Ordförrådet växer i vårt modersmål och om vi så önskar kan vi när som helst under livet lära oss nya språk. Bakom denna förmåga ligger en flexibel och dynamisk språkförmåga som bör beskrivas även på neural nivå. När vi använder ord, förfogar vi både över deras fonologiska form och betydelse (semantik). Då vi lär oss nya ord bör nya fonologiska former och betydelser införlivas i vårt ordförråd, det sk. mentala lexikonet. Hur denna process går till beskriver samtidigt hur informationen är lagrad i denna minnesstruktur. Vidare, genom att granska hur vi förvärvar oss nya ord tillsammans med ny grammatik, eller lär oss gestalta en främmande fonologi, kan man beskriva de processer som sker då man lär sig ett helt nytt språk. I föreliggande avhandling ingår fem studier vilka representerar dessa ovan beskrivna fenomen. I studierna användes magnetenkefalografi (MEG) och funktionell magnetresonanstomografi (fMRI) för att avläsa neural aktivering.

En långvarig psykolingvistisk fråga berör hur grammatisk information bearbetas i hjärnan. Studie I behandlar denna fråga genom att undersöka till vilken grad stimulusmaterialet och val av hjärnbildningsmetod påverkar resultaten. Då verb och substantiv benämndes från identiska bilder, uppstod i stort sätt lika neural aktivering, medan benämning ifrån olika bilder gav upphov till skillnader i hjärnaktiveringen mellan respektive ordklass. Resultaten tyder på att bildens innehåll påverkar den neurala bearbetningen mer än den grammatiska kategori orden tillhör. De viktigaste resultaten erhöles både med fMRI och MEG, även om skillnader mellan dessa två avbildningsmetoder kan ses speciellt då resultaten analyseras på individnivå.

I studie II granskades verbal inläring av namn och betydelser för okända föremål. Hjärnaktiveringen som uppstod vid bildbenämning av bekanta och nyinlärda föremål tydde på att de nya orden blivit välintegrerade i det mentala lexikonet. Resultaten visade emellertid också att fonologisk och semantisk information bearbetas olika i hjärnan då vi yttrar ord. I en uppföljande studie (III), spårades långtidslagring av de nya orden, med upprepade MEG mätningar efter en, fyra och åtta veckor samt tio månader senare. Resultaten visade att en modulering i den neurala aktivering i vänstra tinnings- och pannloberna, under den första veckan var avgörande för huruvida de nyinlärda orden framgångsrikt kunde återkallas tio månader senare.

I studie IV, undersöktes språkproduktion av ett nyinlärnt miniatyrspråk genom att jämföra meningar med ordpar. Att konstruera en mening kräver att ord kombineras med passande syntaktiska komponenter, medan benämning av ett ord-par saknar syntaktisk bearbetning. Resultaten från MEG mätningen antydde att den extra ansträngning som ett nytt språk för med sig är begränsad till planeringsskedet av meningen eller ordparet. Detta reflekterades framförallt i ökad aktivering i hjässloben och vinkelvindlingen (gyrus angularis) då miniatyrspråket jämfördes med modersmålet. Att bearbeta den syntaktiska informationen i meningar påverkade däremot både planerings- och förverklingsskedet. Här antas speciellt den högra tinningsloben spela en viktig roll vid integreringen av enskilda ord och syntax till en enhetlig mening.

Att lära sig ett nytt språk innebär också att man lär sig förstå och producera ett främmande uttal med medföljande fonotaktiska regler. I studie V undersöktes huruvida

långtida inlärningseffekter för främmande fonologi (Koreanska) kan skapas utan medveten inläring då man upprepade gånger hör samma stimuli. Resultatet jämfördes med en liknande uppläggning med upprepade pseudo-ord på modersmålet. Att lyssna och upprepa samma ord flera gånger gav upphov till både neurala och betevidarella inlärningseffekter som även var uppenbara följande dag. Eftersom dessa resultat var lika för både det främmande språket och modersmålet, tolkades inläringen spegla minnet för de hela ordformerna framom en internalisering av de främmande Koreanska fonotaktiska reglerna.

Föreliggande avhandling, sammanfattar flera språkliga element så som fonologi, semantik och grammatik i en dynamisk beskrivning om hur språket bearbetas i hjärnan. Samtliga studier belyser språkproduktion vilket är en väsentlig del av vårt språkbruk, men som länge varit underrepresenterad i hjärnavbildningsstudier.

Abstract

The human language-learning ability persists throughout life, indicating considerable flexibility at the cognitive and neural level. This ability spans from expanding the vocabulary in the mother tongue to acquisition of a new language with its lexicon and grammar. The present thesis consists of five studies that tap both of these aspects of adult language learning by using magnetoencephalography (MEG) and functional magnetic resonance imaging (fMRI) during language processing and language learning tasks.

The thesis shows that learning novel phonological word forms, either in the native tongue or when exposed to a foreign phonology, activates the brain in similar ways. The results also show that novel native words readily become integrated in the mental lexicon. Several studies in the thesis highlight the left temporal cortex as an important brain region in learning and accessing phonological forms. Incidental learning of foreign phonological word forms was reflected in functionally distinct temporal lobe areas that, respectively, reflected short-term memory processes and more stable learning that persisted to the next day. In a study where explicitly trained items were tracked for ten months, it was found that enhanced naming-related temporal and frontal activation one week after learning was predictive of good long-term memory. The results suggest that memory maintenance is an active process that depends on mechanisms of reconsolidation, and that these process vary considerably between individuals.

The thesis put special emphasis on studying language learning in the context of language production. The neural foundation of language production has been studied considerably less than that of perceptive language, especially on the sentence level. A well-known paradigm in language production studies is picture naming, also used as a clinical tool in neuropsychology. This thesis shows that accessing the meaning and phonological form of a depicted object are subserved by different neural implementations. Moreover, a comparison between action and object naming from identical images indicated that the grammatical class of the retrieved word (verb, noun) is less important than the visual content of the image. In the present thesis, the picture naming was further modified into a novel paradigm in order to probe sentence-level speech production in a newly learned miniature language. Neural activity related to grammatical processing did not differ between the novel language and the mother tongue, but stronger neural activation for the novel language was observed during the planning of the upcoming output, likely related to more demanding lexical retrieval and short-term memory.

In sum, the thesis aimed at examining language learning by combining different linguistic domains, such as phonology, semantics, and grammar, in a dynamic description of language processing in the human brain.

1. Introduction

“As the cool stream gushed over one hand she spelled into the other the word water, first slowly, then rapidly. I stood still, my whole attention fixed upon the motions of her fingers. Suddenly I felt a misty consciousness as of something forgotten — a thrill of returning thought; and somehow the mystery of language was revealed to me. I knew then that “w-a-t-e-r” meant the wonderful cool something that was flowing over my hand. That living word awakened my soul, gave it light, hope, joy, set it free!”

Helen Keller, The Story of My Life (1903)

The quotation above describes the revelation of making the conceptual link between a symbolic form and its referent. Presumably, all of us have experienced this revelation when learning our very first words. However, unlike Helen Keller, most of us do not remember this experience. Due to illness, Helen Keller was left deaf and blind at the age of 19 months (Keller, 1903). As a result of this sensory deprivation, her communication skills became extremely underdeveloped. It was not until the age of seven, when she was taught a touch-based sign language, that she suddenly made her language debut and was able to recollect the experience later.

Making the connection between a sound (or a sign) and a referent is, however, not as unique and cataclysmic as one might initially think. On the contrary, our vocabularies are constantly updated (for example, the word ‘blog’ has most likely been learned quite recently) and the process of learning words is so automated that we seldom pay much attention to it in everyday life. But the “mystery of language”, as Keller calls it, prevails for language is more than acquiring links between words forms and their referents. It is through the combination of a large set of words according and a small number of grammatical rules that the human language reaches its unique and seemingly unlimited expressive power. Human language allows for simulation of the future, and for learning from other people’s experiences in a way no other animal can. This has given humans a very powerful evolutionary advantage (Suddendorf, Addis, & Corballis, 2009). Accordingly, the human brain has evolved to manage this computational challenge and several brain areas have become functionally specialized to process linguistic information (see Chapter 1.3.).

The human brain not only needs to handle the computations of combining words into sentences, but also to initially acquire the components of the language itself. The approximately 7000 natural languages with contemporary speakers in the world today (Lewis, 2009) have considerable differences in their syntax, sound systems, and vocabulary. Impressively, despite the genetic variability, all human beings are able to master any one of them as their mother tongue or as a second language. This requires extraordinary flexibility of the human cognitive and neural abilities. This flexibility or plasticity in the child brain motivated one of the most widespread theoretical claims on language learning to date, namely that languages should be learned when the brain is optimally tuned to acquire them in early childhood, i.e., during the so-called critical period (Lenneberg, 1967). Given the theoretical and practical importance of first language acquisition in childhood, it is understandable that it has attracted most research interest. Less is known about the neurocognitive mechanisms of language learning in

the more developed language systems, such as those of adults. Language learning is, nevertheless, not limited to childhood. As mentioned above, the vocabulary of our mother tongue continues to grow throughout one's life, and many people successfully learn new languages as adults. Indeed, it has been estimated that at least half of the world's population speaks more than one language (Grosjean, 1982). The focus of the present thesis is on adult language learning and its neural implementations.

1.1. Linking names to meanings to grammar

Language is a diverse phenomenon that can be studied in many ways depending on what questions one seeks to answer. In linguistics, the aim is to describe what language is like, whereas psycholinguists try to model how language is put to use (Schönefeld, 2001). The neuroscientific perspective on psycholinguistics additionally seeks to understand how language is represented in the brain. One way to do this is to explore neural activation during task performances that tap different aspects of language, such as phonology (the form), semantics (the meaning), or the grammatical rules that govern language. Understanding how these “building blocks” of language (Figure 1) are processed temporally and spatially in the brain is the first step towards describing human language abilities at the neural level. This approach should be complemented by studies on language learning in order to highlight the dynamics of these components when new linguistic information is integrated into the system. In the next chapters, models of language processing as well as previous neuroimaging literature are reviewed with respect to the relevant aspects of the present work. As all the studies in the present thesis contain some form of speech production, special emphasis is put on this particular aspect of language use.

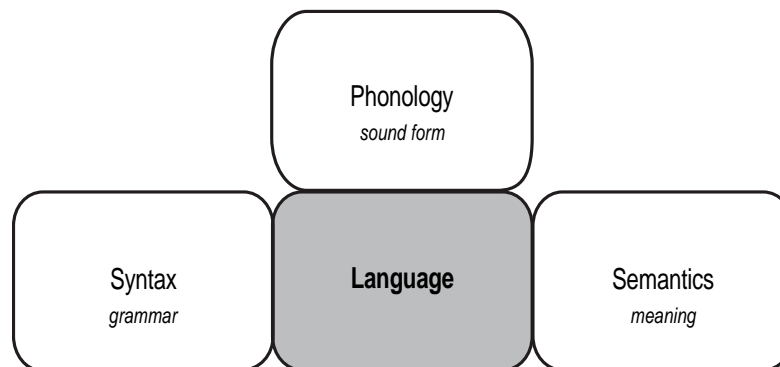


Figure 1. The basic building blocks of language.

1.2. Theoretical views on language processing, memory, and language learning

A model on language processing needs to explain how the listener converts sounds to meanings, and how the speaker converts meanings to sounds. In addition, we need to address the question of what kind of information is stored in the long-term repository of words (mental lexicon) and describe how this information is accessed when language is used real time (Jackendoff, 2007). A viable theoretical framework should also give an account as to how the information in the mental lexicon is acquired and maintained. This requires that models of language processing are related to models of memory. This

chapter first introduces central features of the concept of the mental lexicon and then briefly discusses cognitive models of memory that relate to language learning.

Models of the mental lexicon vary with respect to how linguistic information is structured. In the so-called functional models, phonological and semantic information is viewed as separate levels that are often visualized as “boxes and arrows”, i.e., information-processing units and their interconnections (see, e.g., Harley, 2001; Laine & Martin, 2006). Localist connectionist models seek to define the inner structure and dynamics of such architectures (Dell, 1986; Levelt, Roelofs, & Meyer, 1999) whereas distributed connectionist models view the mental lexicon as a network where phonology and semantics as its emergent properties (Elman, 2004). Models of the mental lexicon vary considerably, among other things, with respect to how they represent grammatical information (Vigliocco, Vinson, Druks, Barber, & Cappa, 2010). Grammatical properties of a word (such as grammatical class) are represented in the long-term lexical store and are automatically retrieved whenever a word is used (Kempen & Hoenkamp, 1987) or not stored in the lexicon but, instead, accessed during the process of integrating a sentence (Jackendoff, 2007; Ullman, 2004). Alternatively, all aspects of linguistic information, including syntax, are emergent properties that (like phonology and semantics) arise from the inherent properties of a distributed network used to model the lexicon (Elman, 2004).

Even though language is often seen as an independent cognitive domain, it is nevertheless intimately linked to the memory systems. The mental vocabulary is thought to be a part of the semantic memory system for general knowledge. Semantic memory and episodic memory for autobiographical events are the subcomponents of the more general declarative memory for facts and events (Squire, 2007). The declarative memory system is typically contrasted with the procedural memory (often also called non-declarative) that is responsible for the acquisition of skills, priming, and implicit associative relationships. This division of memory based on the type of stored information is useful and is supported by independent evidence from both lesion studies and functional neuroimaging of normals (Cabeza & Nyberg, 2000b; Squire, 2007). However, this view needs to be complemented with the functional dimension to describe memory processes in action. For a functional description of memory, three major stages can be differentiated: encoding, maintenance and retrieval (see, e.g., Morris, 2007). For long-term learning to occur, all three stages need to be completed. Without successful encoding, there will be no permanent memory trace. Likewise, a memory trace that has faded or been transformed may indicate a flaw in the maintenance system. Finally, in order to successfully access the memory, appropriate cues are needed, otherwise, the retrieval process will fail.

Learning can occur in a number of situations, but the most relevant distinctions for language learning concern the learning environment, i.e., how deliberate and how effortful the learning is. For example, formal learning usually occurs in a school setting with clearly defined roles for teacher and pupil, and explicit information is given about the grammatical rules, the meaning of novel words etc. In contrast, informal learning occurs when a person freely interacts with the environment.

Very little is known about the maintenance stage of memory as the relevant data mostly comes from the retrieval stage. Consolidation refers to an intermediate stage between the short-term and the long-term representations when the memory traces stabilize to

their final form (Dudai, 2007). Sleep has been shown to drive the consolidation of newly learned information in memory (Diekelmann & Born, 2010). In language learning it has been shown to be an important factor for successful consolidation of newly learned words (Dumay & Gaskell, 2007). Based on the known molecular mechanisms of the consolidation phase, it was originally assumed that once a memory trace is consolidated by neural-level protein synthesis, it is securely stored in the long-term memory (LeDoux, 2007). However, animal studies have shown that memories may be subject to changes each time they are retrieved (Nader & Hardt, 2009). This so-called reconsolidation phenomenon indicates that the memory trace is much more dynamic than initially thought, and that knowledge is constantly modified by experience (Nadel, 2007).

Successful retrieval of a memory trace requires adequate cues. In spontaneous language production, the idea or concept that one wants to express serves as the cue for retrieving the linguistic content of the upcoming utterance. In experimental studies on language production, output is often elicited by a relevant external stimulus, such as a picture. In a sense, one can compare memory retrieval to a game of charades, where the number and type of cues, in addition to attention and choice of strategy, affect the probability of retrieving a target item or utterance. However, unlike in the game of charades, retrieval of linguistic information is rarely a conscious process. The exceptions are the so-called tip-of-the-tongue experience¹ or using a language in which one is not proficient.

How language is learned, and how the mental lexicon develops, is essentially a question of how the memory mechanisms and language mechanisms interact. The models of language learning tend to focus on how infants “crack the code”, i.e. how they segment words from the continuous speech signal, link them to external referents, and distinguish and produce the language-specific phonemes and grammatical rules (Golinkoff et al., 2000). Some of these mechanisms are also relevant for adult learning. For example, the term ‘fast mapping’ refers to the phenomenon that occurs when a word is acquired on the basis of only a few incidental exposures (Bloom, 2000). Fast mapping seems to occur both in adults and children and applies similarly to novel words and facts. Yet, an arbitrary memory task, such as remembering the placing of a sticker, does not manifest fast mapping (Bloom, 2000).

An important memory mechanism that has been linked particularly to word learning, also in adults, is the phonological loop in Baddeley and Hitch’s model of working memory (Baddeley, 2000; Baddeley & Hitch, 1974). According to Baddeley, Gathercole & Papagno (1998), the main function of the phonological loop is the acquisition of novel phonological forms, transferring lexical-phonological information into long-term memory (Baddeley, et al., 1998). Supporting this notion, the capacity of the phonological loop, often measured by the ability to repeat nonwords and verbal sequences, appears to be a good predictor of vocabulary learning (French, 2006; Service & Kohonen, 1995). In this model, the phonological store contains an accurate but brief record of any potentially novel word input. Long-term representations of words would then build up incrementally over time as the result of repeated exposures to novel words at different occasions. This model thereby explains why we can acquire a single unified

¹ The tip-of-the-tongue (TOT) experience refers to a situation where a person knows what word he/she wants to say (i.e., has retrieved the meaning) but cannot retrieve the precise or the full phonological form, thus the expression ‘I have it on the tip of my tongue’. An interesting aspect of the TOT state is that people can often report the initial phoneme, or the number of syllables of the intended word.

phonological representation of a word, in spite of different speakers, accents, and contexts in the learning situations.

A common misconception is that adults are not as good language learners as children. This notion may originate from the critical period hypothesis, which drew parallels between the frequently coinciding milestones of language development and brain development (especially the evolvment of hemispheric lateralization) (Lenneberg, 1967). Lenneberg tried to answer the question why children acquire the mother tongue during a limited period in their development (between 12 months and the early teens). Although he did not specify whether brain maturation also affects second language learning, most studies testing Lenneberg's hypothesis have focused on comparing early and late learners. Still, several confounding factors should be taken into account when children and adults are compared as language learners (Harley, 2001). Firstly, adult learners tend to be less exposed to the new language, compared to children who often are immersed in a new language environment. This also reflects the different learning situations, as adults tend to receive formal learning and children informal. Secondly, adult language learners are often immigrants who are subject to stress, anxiety, depression and other psychological factors that, while common when trying to adapt to a new culture, may affect their learning ability. Comparing second language learners to native speakers is therefore not straightforward.

Considering the issues mentioned above, the data to date suggest that there is no dramatic cut-off in language-learning abilities at the end of puberty. In fact, adults may even have a slight advantage in learning new vocabulary (Harley, 2001). Nevertheless, certain aspects of syntax and phonology may not be fully mastered unless acquired during childhood (Harley, 2001; Kuhl, 2010). These facts speak for a weakened version of the critical period hypothesis, coined as the sensitive period hypothesis, which suggest that at least some aspects of complex syntactic structures are best learned during childhood (Harley, 2001). Still, the issue remains controversial. It has been suggested that even a so-called sensitive period is an overstatement (Rodríguez-Fornells, Cunillera, Mestres-Missé, & de Diego-Balaguer, 2009). One should also bear in mind that similar language performance between early and late learners might have different underlying neural mechanisms.

1.3. Language in the brain

The language network of the brain is mainly left lateralized. Based on the seminal clinicopathological studies during the latter part of the 19th century by physicians Paul Broca, Carl Wernicke and others, the left inferior frontal and superior temporal regions (now known as Broca's and Wernicke's areas) were regarded as the centers for language production and comprehension, respectively. As may be expected, much has happened since the days of these groundbreaking findings in aphasiology. Psycholinguistic models of language have evolved dramatically from the extremely rough distinction between production and comprehension, and with the introduction of modern functional neuroimaging techniques in the latter part of the 20th century, the study of brain-language relationship was no longer limited to lesion studies or behavioral techniques with lateralized stimulus presentations. Using methods such as magnetoencephalography (MEG) and functional magnetic resonance imaging (fMRI), task-related activities of the intact living brain can be measured in space and time, thus revealing both the location and temporal dynamics of the areas engaged by a given task.

More recently, there has been an increasing emphasis also to describe the interplay of different brain areas over time when a task is being performed. The next section gives a brief review of the literature on the neural underpinnings of language, with a special emphasis on findings that are particularly relevant to the present thesis.

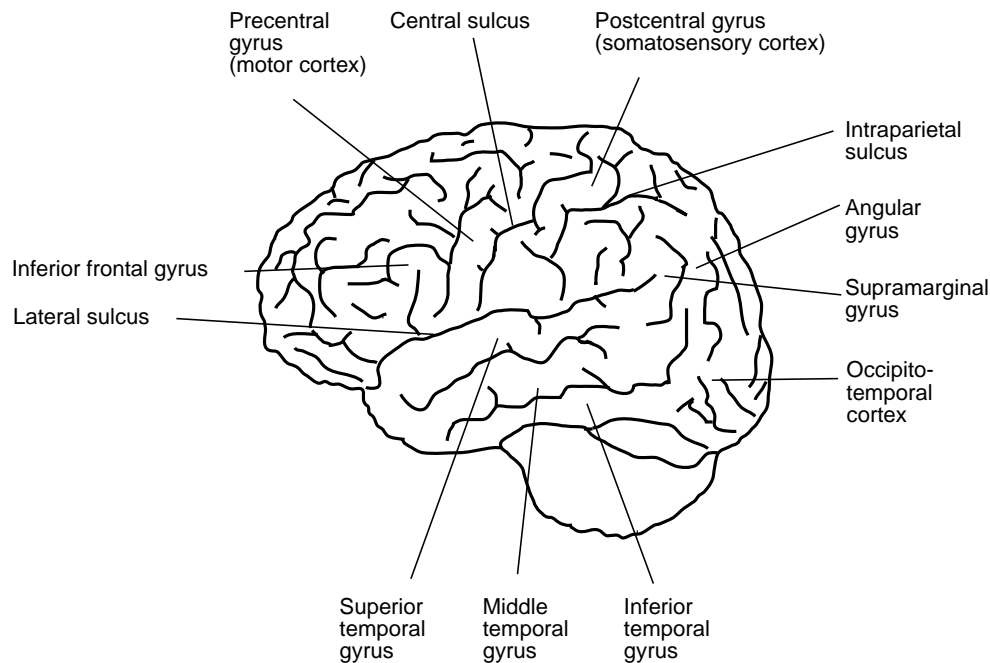


Figure 2. Language involves many different regions of the brain: this schematic picture shows some of the language-related regions in the left hemisphere referred to in the following sections.

1.3.1. Neural representation of the mental lexicon

Models of the mental lexicon provide a theoretical view on how lexical information may be represented in the mind, but in most instances the models claim very little about their neural instantiation. One suggestion is that the words in the mental lexicon would be represented in the brain as distributed neural networks that, during acquisition, link together all relevant information through basic neurobiological learning mechanisms, such as long-term potentiation (Pulvermüller, 1999).

This line of thinking applies well to the neural representation of word meanings. In a distributed network, semantic representations may be organized according to their attributes (Thompson-Schill, 2003). Semantic categories such as faces, tools, buildings and animals have been associated with distinct neural activation patterns in the ventral temporal lobe (Haxby et al., 2001). Studies using verbal material have found a dissociation between living and non-living semantic categories; the most consistent results link the medial occipital cortex to processing of animals and the lateral temporal and premotor cortex to semantic processing of tools (for a review see, e.g., Thompson-Schill, 2003). Studies in which common semantic representations have been sought for pictures and words have reported a range of different regions, including the medial temporal lobe, the anterior part of the left inferior frontal gyrus, the middle and inferior temporal cortex, and the angular gyrus (Binder, Desai, Graves, & Conant, 2009; Bright, Moss, & Tyler, 2004; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996; Vigneau et al., 2006). Neurophysiological studies point to a role for the left temporal

cortex in semantic processing. For example, Maess, Friederici, Damian, Meyer, & Level (2002) found that the effects of semantic category interference in picture naming were observable in left temporal MEG responses at 150-225 ms after picture onset. In receptive language tasks the so-called N400 response² that is thought to index lexical-semantic integration has been located to the superior temporal cortex (Hagoort, 2008; Helenius, Salmelin, Service, & Connolly, 1998; Marinkovic, 2004; Service, Helenius, Maury, & Salmelin, 2007; Vartiainen, Parviainen, & Salmelin, 2009) .

With respect to the neural representations underlying phonological word forms, the results are relatively consistent across methods and modalities; some of these areas are also identified in studies of semantic processing (Vigneau, et al., 2006). There is a wide consensus on the critical role of the superior temporal gyrus in phonological processing (Graves, Grabowski, Mehta, & Gupta, 2008; Hickok, 2009; Indefrey & Levelt, 2004; Salmelin, 2007; Vigneau, et al., 2006). A functional distinction has been made between the superior temporal gyrus which is suggested to be part of an auditory-motor loop, and the adjacent supramarginal gyrus that has been related to phonological loop functions (Vigneau, et al., 2006). Electrophysiological studies have in turn given a time line to the different stages of auditory processing. Phonological analysis of spoken words starts in the superior temporal cortex at 100-200 ms after stimulus onset (Salmelin, 2007), whereas the phonological code is retrieved roughly between 200-400 ms post stimulus in picture naming, word generation or reading (Indefrey & Levelt, 2004; Salmelin, 2007). The posterior part of left inferior frontal gyrus has also been implicated in phonological processing (Bookheimer, 2002; Hagoort, 2005; Vigneau, et al., 2006; Vihla, Laine, & Salmelin, 2006).

One of the key differences between different lexical models is the nature of the relevant information; specifically, to what extent grammatical information is part of the lexicon. Neuropsychological evidence exists for a double dissociation between verb and noun naming impairment in aphasic patients (Caramazza & Hillis, 1991; Miceli, Silveri, Villa, & Caramazza, 1984; Zingeser & Berndt, 1988, 1990). Lesion studies of such patients suggested that particularly the left frontal lobe is related to verb retrieval, whereas noun retrieval is compromised especially after damage to the left anterior temporal cortices (Damasio & Tranel, 1993). However, more recently it has been claimed that the grammatical category might not be stored with the word-form, but be assigned by morphosyntactic processes (Shapiro & Caramazza, 2003; Shapiro, Moo, & Caramazza, 2006). When controlling both for the access to semantic features and the inflectional morphology specific to each grammatical class, the dissociation in the neural activation to verbs and nouns (verb: left prefrontal and superior parietal lobule; nouns: left anterior fusiform gyrus) appeared also for pseudowords, and was could attributed to grammatical processing.

However, more recent studies have questioned the specificity of the lesion findings (Matzig, Druks, Masterson, & Vigliocco, 2009), and some neuroimaging studies indicate that the same general cortical network is activated for both verbs and nouns (Siri et al., 2008; Sörös, Cornelissen, Laine, & Salmelin, 2003; Tyler, Russell, Fadili, & Moss, 2001). It has also become clear that verbs and nouns differ in many ways other

² The N400 response is named after a negative deflection seen in electroencephalography (EEG) that peaks at around 400 ms post stimulus. A typical N400 paradigm presents sentences that end with an expected or unexpected word, e.g., *The pizza was too hot to eat/sing*. An anomalous sentence-final word elicits a stronger N400 response than the expected word (Kutas & Hillyard, 1980).

than their grammatical roles and that factors like the age-of-acquisition, word frequency (Gentner, 1982) and imageability (i.e. the ease with which a word evokes a mental image) (Bird, Howard, & Franklin, 2000) should be taken into account when studying verb and noun processing. These findings gave rise to the idea that the apparent dissociation between nouns and verbs may stem from semantic differences between words for actions and objects, irrespective of their grammatical class. Vigliocco and colleagues (2006) showed that Italian nouns and verbs related to motor movement (e.g. '*corsa*', the run, '*correre*' to run) activated the left precentral gyrus irrespective of grammatical class and that words related to a sensory modality (e.g. '*gusto*', the taste, '*gustare*', to taste), activated the left inferior temporal and frontal regions, again regardless of grammatical class. Thus, the same underlying neural network would be active for all words, but the type of activation would depend on e.g., semantic features (Davis, Meunier, & Marslen-Wilson, 2004; Vigliocco, et al., 2006), task complexity (Siri, et al., 2008) or different morpho-syntactic processing demands (Tyler & Marslen-Wilson, 2008).

1.3.2. Adult language learning and its neural correlates

Our knowledge of the neurocognition of language learning in adults is still rather limited, as the main research emphasis has been on language acquisition in childhood. While there is evidence that the learning mechanisms applied by children, such as fast mapping (Bloom, 2000) and statistical learning (Saffran, Aslin, & Newport, 1996) remain available in adulthood, the learning process may be different when new lexical information is integrated into a store that already contains a vast amount of entries.

One theoretical account of the underlying neural mechanism of word learning suggests that it occurs in two stages: rapid initial acquisition supported by medial temporal and hippocampal learning and slower neocortical learning achieved by offline consolidation of previously acquired information (Davis & Gaskell, 2009; McClelland, McNaughton, & O'Reilly, 1995). This has been coined as the Complementary Learning Systems (CLS) model. An important feature of the model is that the rapid memory system uses sparse and independent representations to store unique and context-specific episodes. As the underlying representations become more distributed and overlapping, the representation is generalized beyond a specific context and turns into a semantic memory. When the model was adapted to word learning, over-night sleep was shown to be an explanatory factor for successful consolidation of memories (Davis & Gaskell, 2009). Typical learning paradigms assess short-term effects that arise during the course of the experiment, but do not address the long-term integration of a new item into the lexicon. However, if participants are allowed to sleep in-between learning and the recall tasks, the cortical activation becomes akin to familiar words. In contrast, if the participants learn the words on the same day as the scanning (and, therefore, do not sleep between learning and retrieval) their neural activation of the newly learned words is more similar to non-trained words (Davis, Di Betta, Macdonald, & Gaskell, 2009).

The CLS model of word learning has been evaluated mainly through studies that have contrasted either brain activity during encoding and subsequent behavioral recall or the neural responses to familiar and unfamiliar pseudowords (Davis & Gaskell, 2009). For example, activation in the medial temporal and left parietal cortex during word-picture association has been shown to be predictive of recall success after scanning (Breitenstein et al., 2005). The medial temporal cortex (specifically the

parahippocampal gyrus) has also been linked to the encoding phase in a contextual learning paradigm, where participants inferred the meaning of a novel word gradually from three different sentence-contexts (Mestres-Missé, Camara, Rodríguez-Fornells, Rotte, & Münte, 2008). Using electroencephalography (EEG) the same authors found that also the N400 response, linked to lexico-semantic integration, incrementally became more and more similar to familiar items as each of the three sentences were presented (Mestres-Missé, Rodríguez-Fornells, & Munte, 2007). All three studies have been interpreted to support the CLS model (Davis & Gaskell, 2009).

A brief review of vocabulary acquisition studies using picture naming provides some further support for a two-stage memory system, with different neural systems underlying the two stages. Rabouyeau and colleagues (2004) studied picture naming in the native and second language before and after an intensive period of word training in the second language. The relative activity in the hippocampus and left temporal cortex (among other regions) between the pre- and post-training measurements correlated with the long-term (2 months) proficiency of object naming in the second language. A number of studies on word learning have trained the participants on word-picture pairings over multiple days (Cornelissen et al., 2004; Cornelissen et al., 2003; Dobel et al., 2010; Grönholm, Rinne, Vorobyev, & Laine, 2005, 2007). As the CLS model would predict, the concomitant neuroimaging results highlight neocortical regions. In a PET study, participants were trained on novel tool names for four days; naming the newly learned objects recruited a more extensive network compared to naming familiar objects, namely, the left inferior frontal gyrus, the anterior superior temporal gyrus, and the cerebellum (Grönholm, et al., 2005). MEG studies have found learning effects in the sustained responses between 300-800 ms. Naming of newly learned tool names after four to five daily training sessions showed that novel and familiar items were generally processed in a similar manner, but that accessing newly learned words increased the activation in the left parietal region (Cornelissen, et al., 2004). Dobel et al. (2010) used a similar five-day training procedure, but probed learning with a word-picture priming task comparing trained and untrained pseudowords with familiar words. After training the N400 response in the left temporal cortex to trained words was comparable to that elicited by familiar words (Dobel, et al., 2010). These studies show that learning which takes place over several days modifies neocortical responses, even though there is a certain degree of variation with respect to the exact locations. However, as the studies differ substantially in experimental design (imaging method, task, and stimulus manipulations), it is not surprising that the cortical regions involved do not fully converge.

The studies reviewed above have not sought to evaluate the stability of newly learned lexical representations after the training has been completed. Word learning studies in which the retrieval and encoding stages have been separated by days or even weeks, have focused on changes in brain activation related to the type of information encoded during learning (Grönholm, et al., 2005; Rabouyeau, et al., 2004; Sandak et al., 2004). On the other hand, studies that specifically target long-term maintenance mechanisms have focused on episodic memories that are not related to learning of new phonological or semantic information (Bosshardt et al., 2005; Habib & Nyberg, 2008; Paller & Wagner, 2002; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). Accordingly, studies that evaluate the formation of permanent word representations and their level of lexical integration over the course of several months have been lacking.

As noted above, the phonological loop mechanism in the working memory model by Baddeley and Hitch has been strongly linked to word learning (Baddeley, et al., 1998). The main cortical correlates of phonological short-term memory encompass the parietal lobe and the superior temporal cortex, along with inferior frontal and premotor areas which have been associated with subvocal rehearsal (Baddeley, 2003; Buchsbaum & D'Esposito, 2008; Jonides et al., 1998; McGettigan et al., 2010; Paulesu, Frith, & Frackowiak, 1993). However, the function of the phonological store depends on the way speech is processed at the sensory level (Buchsbaum & D'Esposito, 2008), i.e. the specific location for the phonological loop depends on the task at hand. For example, listening to repeated spoken words tends to decrease the activity in the frontal and superior temporal cortices (Graves, et al., 2008; Majerus et al., 2005; Rauschecker, Pringle, & Watkins, 2008), whereas encoding or retrieving newly learned phonological word forms may increase activation in the parietal lobe (Breitenstein, et al., 2005; Cornelissen, et al., 2004; Cornelissen, et al., 2003). At a cognitive level, these task effects suggest that the superior temporal areas are engaged in echoic aspects of word perception, whereas parietal lobe activation may reflect more rehearsal-based phonological short-term memory (Buchsbaum & D'Esposito, 2008; McGettigan, et al., 2010).

When learning a foreign language, one of the most demanding aspects is to learn to perceive and produce the nuances of the novel phonology. Acquisition of a word in a foreign language requires a link between the new name and the meaning, but also a novel sensory-motor representation, which is used for producing the new word (Buchsbaum & D'Esposito, 2008). Learning by rehearsing non-native phoneme sequences has been shown to decrease frontal activation as a function of familiarity and exposure, which has mainly been interpreted as reflecting less demanding motor and articulatory planning (Klein, Watkins, Zatorre, & Milner, 2006; Moser et al., 2009). Another approach is to study brain activation related to perceptual aspects of spoken word processing. The so-called repetition suppression effect refers to the typical decrease in neural activation that occurs with repeated exposure to stimuli (Grill-Spector, Henson, & Martin, 2006). As learning most often occurs by repeated exposure to language, recording the brain activation while participants listen to a novel language is a straightforward way to study phonological learning. Using this approach, phonological processing and learning have been linked to repetition-induced suppression in the left superior temporal cortex (Graves, et al., 2008; Majerus, et al., 2005; Rauschecker, et al., 2008). The same effect has also been observed in the inferior frontal and premotor areas, suggested to signal decreased demands on articulatory and integrative processing (Klein, et al., 2006; Moser, et al., 2009; Rauschecker, et al., 2008). However, to be master a lexicon for a novel language, the sensory-motor representations of novel words need to be sustained long-term and the phonotactic regularities need to be internalized (Saffran, Newport, Aslin, Tunick, & Barrueco, 1997).

Mastering a new language also means fluent command of the grammatical rules of the language. The declarative/procedural model (Ullman, 2001a) argues that processing of syntax and lexical knowledge are supported by different neural systems. Rooted in frontal/basal-ganglia structures, the procedural memory system would operate on the rules of the language, whereas temporal and temporo-parietal structures would be active when processing word knowledge, attributed to declarative memory (Ullman, 2001a, 2004). In addition, it is suggested that this division of labor changes with age so that

adult language learners would also rely more on declarative memory for grammar (Ullman, 2001b). However, others have suggested that it is the proficiency rather than the age of acquisition that determines the processing mechanisms of the second language (Friederici, Steinhauer, & Pfeifer, 2002; Rodríguez-Fornells, et al., 2009) and that the first and the second language are processed by the same neural devices (Perani & Abutalebi, 2005). For example, Golestani et al. (2006) found that the higher the grammatical proficiency was in the second language, the more akin to the first language was activation of the left inferior frontal gyrus in sentence production. The authors noted that this finding may reflect stronger engagement of the procedural memory in the highly proficient than less proficient bilinguals.

One way to study second language acquisition is to train participants with an artificial miniature language and then measure neural activity when the participants process the novel language. Using this approach, increased activation in the left inferior frontal gyrus during learning has been found to correlate with increased proficiency (Newman-Norlund, Frey, Petitto, & Grafton, 2006; Opitz & Friederici, 2003). The authors noted that acquisition of a miniature language within a relatively short time period may even elicit syntactic neural activation which resembles that of the mother tongue. Further support for this idea was found with EEG, with similar P600 responses to syntactic violations both in a newly learned miniature language and the native language (Friederici, et al., 2002; Mueller, Hahne, Fujii, & Friederici, 2005).

Comparing the models on language learning shortly reviewed above (the CLS, the working memory, and the declarative/procedural model) one may notice that they address slightly different aspects of language acquisition. The CLS model describes a two-stage learning process, with functionally different roles for initial acquisition and long-term consolidation of lexical representations, including both their phonological and semantic forms (Davis & Gaskell, 2009). In contrast, the working memory model focuses on acquisition of specifically phonological word forms (but possibly also syntactical knowledge) with the help of the phonological loop (Baddeley, et al., 1998). However, both models attribute a role for echoic memory in incremental building-up of long-term representations. The declarative/procedural model, on the other hand, makes a division between the memory systems supporting lexical and grammatical processing and suggests qualitative differences between first and second language acquisition (Ullman, 2001b). The underlying neural implementation of language learning is an essential part of both the declarative/procedural and the CLS model. The models converge in emphasizing the medial lobe as a mediator in the formation of new words whereas consolidated long-term representations are reflected by more independent neocortical processing e.g. in the left temporal lobe. In contrast, the working memory model was originally developed to explain clinical symptoms and behavioral data, and the neural level has been added later. In a recent attempt to integrate different views of language learning into detailed functional-anatomical model of language learning incorporates the medial temporal lobe contribution to initial storage and subsequent consolidation of new linguistic information, a working-memory related dorsal l cortical system for phonological learning, and a ventral frontotemporal system for meaning inference and acquisition (Rodríguez-Fornells, et al., 2009). Moreover the model incorporates more general brain systems related to cognitive control, inductive reasoning and motivation that all play a role in language learning.

In sum the experimental studies addressing the neural correlates of new language learning in adults is still quite limited, but the available evidence indicates the engagement of various predominantly left hemispheric regions in these learning processes, depending on the nature of the learning task and the learning phase studied. Previous studies on adult language learning have generally focused on only one aspect of linguistic knowledge, for example, learning a new name or a new meaning, but seldom both. This is in part also reflected in the theoretical models. Using a novel miniature language approach facilitates comparison of word versus grammar learning, which is directly related to the predictions of the declarative/procedural model. However, to date such studies have focused on general effects of language processing between native and second-language speakers. For the most part, neural learning effects have been evaluated either during or after training, whereas long-term studies that encompass all memory stages from encoding to maintenance and retrieval are lacking.

2. Aims

The main aims of this thesis were to investigate language learning in adults when expanding vocabulary in the mother tongue and learning a new language. Specifically, the thesis explores phonological, semantic and syntactic aspects of language processing at the level of the brain. It also ties together language processing and memory mechanisms, as both are involved in language learning. The specific goals for each study were as follows:

- i. To investigate whether verbs and nouns are subserved by different neurocognitive mechanisms or whether differences observed in previous studies could at least in part be related to differences in the picture content. The study also evaluated the convergence between two different imaging methods (MEG and fMRI) with respect to a high-level cognitive task, picture naming.
- ii. To investigate how new words of the mother tongue are integrated into the mental lexicon and how this manifests at the neural level in picture naming. Processing of phonological versus semantic information related to newly learned lexical items was explicitly probed by two separate categorization tasks for these domains.
- iii. To explore the long-term memory mechanisms of newly acquired words in the mother tongue over a follow-up period of 10 months, with four post-learning measurements.
- iv. To study production of words, with and without sentence context in a newly learned miniature language and in the mother tongue.
- v. To study the incidental learning effects of repeated exposure to word forms in a foreign phonology compared to pseudoword exposure in the mother tongue, tracking the stability of the effect to the following day.

3. Methods

3.1. Participants

Altogether 42 native Finnish speakers participated in the studies. Informed consent was acquired from all participants. The studies were all approved by the local ethics committee. The mean age was 26 years, ranging from 19 to 44 years, and the vast majority were right-handed (confirmed by the Edinburgh handedness inventory, (Oldfield, 1971) in Studies II-V). One participant was self-reportedly ambidextrous. Both genders were equally represented in the participants of studies II-IV. In study I, one participant was excluded for bad MEG data quality and only data from the remaining four females and seven males were used in analysis. Participants reported no neurological disorders or diagnosed learning disabilities. Their educational backgrounds varied from upper secondary school to university level degrees. For studies with visual stimuli (Studies I-IV), normal (or corrected to normal) vision was required and for Study V, which contained auditory stimuli, participants reported normal hearing. Study III was a follow-up investigation of Study II and, thus included the same sample of participants.

3.2. Experimental stimuli and material

3.2.1. Study I: Pictures of actions and objects

In Study I, the choice of stimuli was of paramount importance as one of the key questions was whether different the types of pictures used for action and object naming would affect the way the word classes are processed. A set of 100 pictures were chosen that allowed naming of either the action or the object from the same image. A control set of object-only images was then constructed by dissolving the action into arbitrary lines in the background, thereby keeping the same visual complexity between the two sets of pictures. The majority of the action images were derived from the study of Sörös and colleagues (2003).

The naming consistency for both the actions and the objects used by Sörös and colleagues (2003) was established in a separate behavioral test with six naïve participants who did not participate in the actual study. The noun and verb depicted by an image had different word stems, although they were often conceptually related, e.g., to drink – a glass. The target verbs and nouns were matched for word frequency and number of syllables.

3.2.2. Studies II & III: Pictures of previously unknown tools

The same set of 200 drawings of real but old or rarely used tools and utensils and a set of 50 familiar tools were employed in both Study II and Study III. All images were visually similar simple black-and-white drawings. Visual complexity was tested in a behavioral pre-test on eight naïve Finnish participants (who did not participate in either study); their ratings did not differ between the stimulus categories.

The old tools and their images were derived from an ethnological dictionary and have been used in several language learning experiments (Laine & Salmelin, 2010). Most of the tools were related to farming or seafaring and are unknown to modern-day humans. As confirmed by the pre-test, their usage cannot be deduced from the visual form. The

stimuli were divided into four categories depending on what type of information was presented during the training sessions. Either both the name and a brief definition describing the use of the object were given (Name & Definition), or alternatively only the name (Name) or the definition (Definition). One fourth of the novel objects were presented during the training without any information (No Name). Pictures of familiar objects (Familiar) as the control condition were included in all the task and training phases.

3.2.3. Study IV: Anigram—a miniature language

For Study IV, a miniature language called Anigram (animals + grammar) was constructed that contained 20 nouns (all animal names), 10 verbs (transitive verbs depicting easily visualized actions) and three grammatical rules for object marking. The nouns are arbitrarily divided into three genders: nouns ending in -a/-y are regarded as feminine, nouns ending with -u/-i masculine and nouns ending with -e/-o neutral. The object in a sentence is marked by a morphological suffix (-s, -r or -k) determined by the subject gender. For example, the feminine subject *dosuda* (bear) triggers the object marker -s on *tunuke* (cow), as in the sentence *dosuda benosa tunukes* (the bear hits the cow). This type of object marking does not occur in Finnish or in most indo-European and Romance languages (e.g. Swedish, English, German or French). Confounding factors due to transfer effects from another language were thus controlled for, as the participants could not learn the rules by generalizing from a known language.

The participants also performed the experimental task in their mother tongue, Finnish. In Finnish the object is, similarly to Anigram, marked by a suffix (-a, -ä, -ta or -tä). Unlike Anigram, the case in Finnish is determined by the verb phrase. In this study the verb phrase always called for the partitive³ case of the object. Also, in Finnish, inflected words sometimes undergo morphophonological variation, for example *moose* in the nominative singular form is *hirvi*, but in the partitive singular form becomes *hirveä* where the final phoneme in the stem has changed from -i to -e.

Black-and-white cartoons of two animal characters, either engaged in an action (e.g., a bear hitting a cow) or passively standing next to each other (e.g., bear, cow) were used both for training and for evaluating neural effects of language learning.

3.2.4. Study V: Spoken Korean words and Finnish pseudowords

In Study V, learning of novel phonology, real spoken Korean words were contrasted to pseudowords in Finnish, the participants' mother tongue. The words in both categories were four syllables long and their duration varied between 850–1446 ms in Korean and 1008–1490 ms in Finnish. The time window 0–1200 ms from stimulus onset was used in the MEG analyses. The stimulus set included a total of 400 words that were divided into a Recurring category (five presentations of 100 words), a Nonrecurring category (one presentation of 100 words), and a New category with the remaining 200 words, which were presented only once on the second day of the experiment. The Korean words were spoken by a female native Korean linguist and the Finnish words by a female native Finnish student of speech pathology. The Finnish pseudowords were composed of two-

³ Finnish differentiates between total and partial objects (cf. *I drank the coffee* vs. *I drank (some) coffee*) with nominative/genitive and partitive cases, respectively.

syllable real Finnish words (Lönnrot, 1874-1880) that are no longer in use. It was not possible to deduce a meaning from either the Finnish or Korean stimuli. With the exception of the different female speakers the stimulus sets differed notably only with respect to their novel or familiar phonology.

3.3. Training procedures

Studies II and IV both included computer-assisted training sessions. In Study II the participants were instructed to learn the new names and/or definitions by viewing a pictured object and memorizing any information simultaneously provided (name, usage, both). The Familiar and the No Name objects were presented without any information during all training sessions to ensure equal visual familiarity of all items. All stimuli were presented in a random order. After each training session the amount of learning was evaluated by a paper-and-pencil questionnaire. Daily training sessions (except weekends) continued until participants mastered 98% of the names; in practice this required 3-6 training sessions. Training to a criterion was chosen in order to achieve proficient usage of the new words by all participants and to minimize possible differences caused by natural variation in individual learning ability or strategies.

The miniature language Anigram used in Study IV was trained for four days together with the experimenter. In the beginning of each training session, the grammatical rules of the language were explained and exemplified. The names of the animals and the rules were then trained with the help of black-and-white cartoons and a corresponding written sentence in Anigram. The experimenter first spoke the depicted sentence in Finnish (thereby removing any uncertainties of what the picture portrayed) and then read aloud the same sentence in Anigram. The participant then had to repeat the sentence in Anigram correctly before the experimenter allowed the next example to be presented. Altogether 90 practice images, each presented twice at each session, were used during the training. After each training session, the amount of learning was evaluated by a separate test with previously unencountered stimuli. Another completely new set of cartoons was used in the MEG recording.

Study V did not have a separate behavioral training phase. Instead, an incidental-learning paradigm was used in which participants were exposed to Recurring and Nonrecurring Korean words or Finnish pseudowords during the first MEG measurement. The participants were not instructed to memorize the words in any way, only to repeat what they had heard as accurately as possible. After the second MEG measurement in each language, participants performed an explicit recognition task on a subset of the stimuli mixed with 50 % new items. Participants indicated by button-press if they felt they had encountered the word before. Recognition probabilities were calculated for each category, taking into account the false alarm rate⁴.

⁴ False alarm rate is estimated to take into account the so-called false positives, i.e., when a participant claimed to recognize a stimulus that had not been encountered previously.

3.4. Brain activation measures

3.4.1. Magnetoencephalography

Magnetoencephalography (MEG) is a non-invasive electrophysiological measure of neural activity with excellent temporal (milliseconds) and good spatial resolution (centimeters). In MEG the magnetic fields are not distorted by the skull bone, dura or other non-magnetic material between the source and the sensor. Hence, MEG source localization tends to be spatially more accurate than the related EEG method (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993).

MEG is based on the fact that postsynaptic potentials in synchronously active, similarly aligned (apical dendrites of) pyramidal cells give rise to weak magnetic fields that can be measured outside the head; in order for the signal to be detected, the size of the underlying cell population needs to be in the order of tens of thousands of neurons (Lopes da Silva, 2010; Murakami & Okada, 2006). Because the cranial volume is approximately a spherical volume conductor, currents with a radial orientation are severely attenuated by the volume currents. Therefore, MEG is most sensitive to sources within the cortical sulci (Hämäläinen, et al., 1993) (see Figure 3). In practice, however, it has been shown that source depth rather than orientation is the main limiting factor for the sensitivity of the MEG signal (Hillebrand & Barnes, 2002). In addition, factors such as coverage of the sensor array (e.g., sensors typically do not cover the face and neck

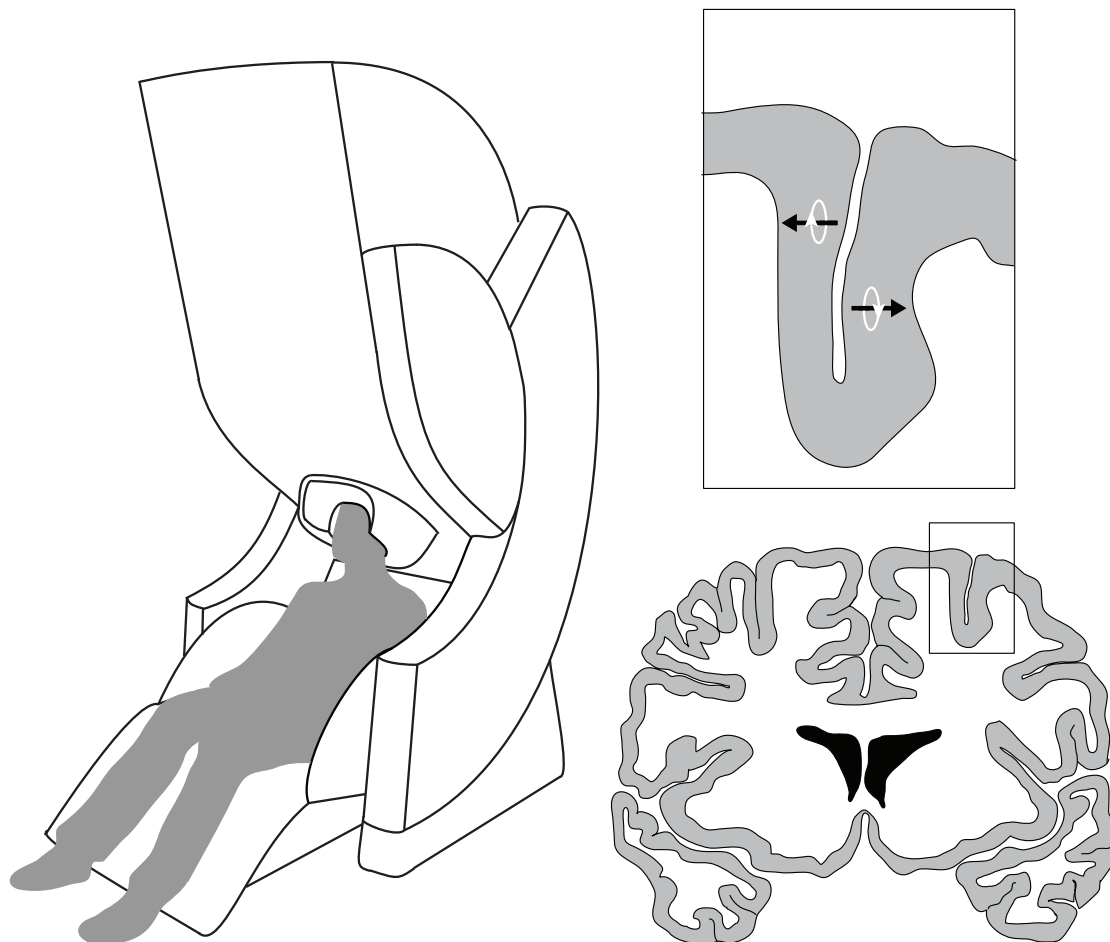


Figure 3. **Left:** Schematic picture of the MEG-device. **Right:** Enlarged sulcus showing the direction of the current flow in pyramidal cells (black arrow) with respect to the cortical surface.

areas fully) and signal-to-noise ratio in measured data contribute to the fact that source-localization accuracy depends on the brain region. In general, currents generated in the prefrontal or deep brain structures seem to have the poorest source localization accuracy (Tarkiainen, Liljeström, Seppä, & Salmelin, 2003).

Source localization refers to the process of decomposing the magnetic field signal into the neural activation that generates the measured signal. This modeling requires solving the inverse problem which, by nature, is ill-posed and has no unique solution. Therefore, certain assumptions must be made about the underlying sources to restrict the number of possible source configuration (Hämäläinen, et al., 1993). In this thesis two different approaches have been used to solve the inverse problem: modeling each source as an independent equivalent current dipole (ECD) or minimizing the norm of the current strength/power for a distributed-source model.

Modeling the neural activation as equivalent current dipoles (Hämäläinen, et al., 1993; Salmelin, 2010) makes a minimal number of assumptions; only that the active cortical patch can be represented as a current dipole where the mean strength and direction denote the net current flow in that area. This assumption is grounded in the physiology as postsynaptic potentials act effectively as current dipoles. The dipolar component is also the most prominent in the MEG signal as the higher-order components decrease more rapidly with distance (Hämäläinen, et al., 1993). The location, orientation and amplitude of an ECD can be determined from a distinct dipolar pattern in the measured magnetic field with a least-squares search. Several ECDs can be incorporated into a multi-dipole model (Salmelin, 2010), where the amplitude of each source is allowed to vary as a function of time, while the orientation and location are typically kept fixed. The explanatory power of the model can be evaluated through the goodness-of-fit value that estimates the percentage of the measured data that is explained by the dipole model at each time point. In this thesis the explanatory power of the multi-dipole model was also evaluated by testing that the trial-to-trial distribution of the remaining residual (the difference between the measured and the predicted data) equals zero-means random noise in the majority of the time points.

Distributed-source modeling approaches express the MEG data with a quasi-continuous distribution of source currents within the brain volume. The source space is first approximated as a grid comprising hundreds or thousands of dipolar sources with unknown amplitudes. The activity in each grid point is then determined by the MEG data and by minimizing the estimate with respect to either the L1 norm (minimum-current estimate, MCE; Uutela, Hämäläinen, & Somersalo, 1999) or the L2 norm (minimum norm estimate, MNE; Hämäläinen & Ilmoniemi, 1994). Amendments to the MNE approach include constraining the grid points to the cortical surface and applying noise-normalization (Dale, Fischl, & Sereno, 1999; Dale et al., 2000; Fischl, Liu, & Dale, 2001).

For quantification purposes, regions of interest can be selected in both the MNE and MCE solutions. The time courses of the estimate can then be quantified, similarly to the time courses of the dipole strengths in ECD modeling, and tested statistically. In Study IV, ECD source localizations are introduced as a way of constraining the selection of regions of interest in the MNE solution.

For the statistical analyses, the time course of an active area was characterized by either its mean or peak amplitude and the latency at which the peak amplitude was reached. Statistical tests were carried out at the group level by repeated measures or one-way analysis of variance. Individual-level testing was carried out either by permutation tests on single-trial activation strengths or by comparing the difference of activation strengths between two conditions to the standard deviation of the prestimulus baseline.

3.4.2. Functional magnetic resonance imaging

Functional magnetic resonance imaging (fMRI) was used as part of Study I to evaluate the convergence of two different brain activation measures on a complex cognitive task. fMRI is a brain-imaging method that provides excellent spatial resolution throughout the brain. The most common form of fMRI exploits the differences in magnetic properties of oxygenated and deoxygenated hemoglobin whose relative concentrations depend on the oxygen consumption of activated neurons. The downside of this so-called blood-oxygen-level-dependent (BOLD) signal is a relatively poor temporal resolution, typically on the order of seconds.

If biological tissue (such as the human brain) is placed in a strong magnetic field, energy at the specific resonance frequency may be absorbed and later emitted by the atomic nuclei. The difference between the absorbed and emitted energy depends on the number and type of nuclei (Huettel, Song, & McCarthy, 2004). In magnetic resonance imaging (MRI), the scanner is tuned to the hydrogen nuclei, which are the most common nuclei in the human tissue (e.g., as part of the water molecule). In a strong static magnetic field (typically 1.5 or 3 Tesla) the spins of the protons in hydrogen nuclei align along the magnetic field. Applying a radiofrequency electromagnetic pulse will make the protons absorb energy, causing their spins to tilt; this is called spin excitation. When the pulse is turned off, the proton spin slowly returns to its original orientation along the magnetic field (spin relaxation) and the released energy gives rise to a measurable signal which, in turn, can be transformed into an image of the brain. During spin excitation, the precession of the proton spin becomes temporarily phase locked. The time it takes for the spins to dephase is called the transverse relaxation time and it is affected by local magnetic field inhomogeneities and the interaction between the spins themselves. The different magnetic properties of oxygenated and deoxygenated hemoglobin affect the transverse relaxation time and these differences underlie the BOLD signal of fMRI (Huettel, et al., 2004).

The fMRI signal can be analyzed in several ways. In the present thesis a classical block-design was used. In block designs, stimuli of the same category are grouped together and the signal from the entire block is statistically tested against the signal from another block. Using a general linear-model approach, statistical parametric maps (SPM) can be calculated using the different block conditions as regressors. The contrast images between different task and/or rest conditions are then subjected to a random effects group-level analysis. As the fMRI image consists of tens of thousands of voxels, each of which undergoes testing against the different experimental conditions, a correction of multiple comparisons is called for. In this thesis a false-discovery-rate (FDR) correction was used with a minimum cluster size criterion.

4. Experiments

4.1. Study I: Naming actions and objects

Picture naming is a common task both for assessing category-specific impairments in patients and in brain-imaging studies on the processing of verbs and nouns. Especially in clinical settings, different types of images have been used; typically, nouns are named from pictures of objects and verbs from pictures of actions that often include a human figure. Yet, the visual properties of the picture stimuli may underlie some of the differences attributed to the word classes (Bird, et al., 2000). This perceptual factor may be overcome by using the same set of action pictures and merely changing the instruction between action and object naming. By additionally using a set of pictures with objects only, the impact of the image on picture naming can be deduced. If visual properties account for the apparent discrepancy between verbs and nouns, the action and object images would result in different patterns of neural activation, regardless of the type of words one seeks to name from them. On the other hand, if grammatical class is processed differently at the neural level, neural processing patterns of accessing verbs and nouns should differ when naming from an identical visual stimulus and object naming should display similar processing patterns irrespective of the stimuli.

This question was studied using two different brain imaging methods, namely MEG and fMRI, thereby enabling a combination of the strong points of each method: the excellent temporal resolution of MEG and the accurate spatial resolution of fMRI. Combining the two methods is, nevertheless, not a straightforward task, as they measure very different aspects of brain activity. The magnetic fields detected by MEG arise directly from the underlying neural currents, whereas the fMRI BOLD signal reflects metabolic changes that follow neural activation. This study also addresses an important methodological question on level of convergence between MEG and fMRI in high-order cognitive brain processing, when the task and participants are the same.

In both the fMRI and MEG measurements the participants named the pictures silently in three blocked task conditions: naming actions from action images, naming objects from action images and naming objects from object images. Between the randomized blocks, 30 second rest blocks were inserted (baseline condition). In the MEG experiment, the same task was additionally performed overtly, providing reaction times for the different conditions.

The results showed that the content of the image, rather than the grammatical class of the retrieved word influenced the cortical activation pattern (Figure 4). Contrasting action images with object images in fMRI revealed that action images, irrespective of the naming instruction, evoked stronger activation in the left middle temporal gyrus, the supramarginal gyrus, the supplementary motor area and the premotor area. These areas have been linked to processing of actions, tool usage or verb processing (Martin, 1996; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Perani et al., 1999; Shapiro, et al., 2006). Similar results were obtained in a separate publication that focused on the fMRI results only (Liljeström et al., 2008).

In MEG, the same comparison between action images and object images showed stronger sustained activation to action images from 250 ms onwards in the left parietal and frontal areas, thereby confirming the results of Sörös et al (2003). A direct comparison of action or object naming from the same images, showed no specific

modulations of activity in either fMRI or MEG. Thus, picture content rather than grammatical class seem to determine whether distinct neural correlates for verbs and nouns can be detected in picture naming.

The group-level convergence between the two imaging methods was generally good, and importantly, the main stimulus effects did not differ between methods. The areas that were observed active with both MEG and fMRI included the bilateral occipito-temporal, parietal, and inferior frontal cortices. Frontal activation was prominent in fMRI and, although it was also detectable in seven out of eleven participants in MEG, more intersubject variability was observed in the latter method. The right middle temporal activation detected by MEG was not evident in fMRI, possibly due to susceptibility artefacts near the ear canals. Conversely, the activation of the supplementary motor area was observed in fMRI but not in MEG. At the individual level, the average difference between the fMRI and MEG source localization was 18 ± 1 mm (ECD) or 19 ± 1 mm (MNE), depending on method of localization.

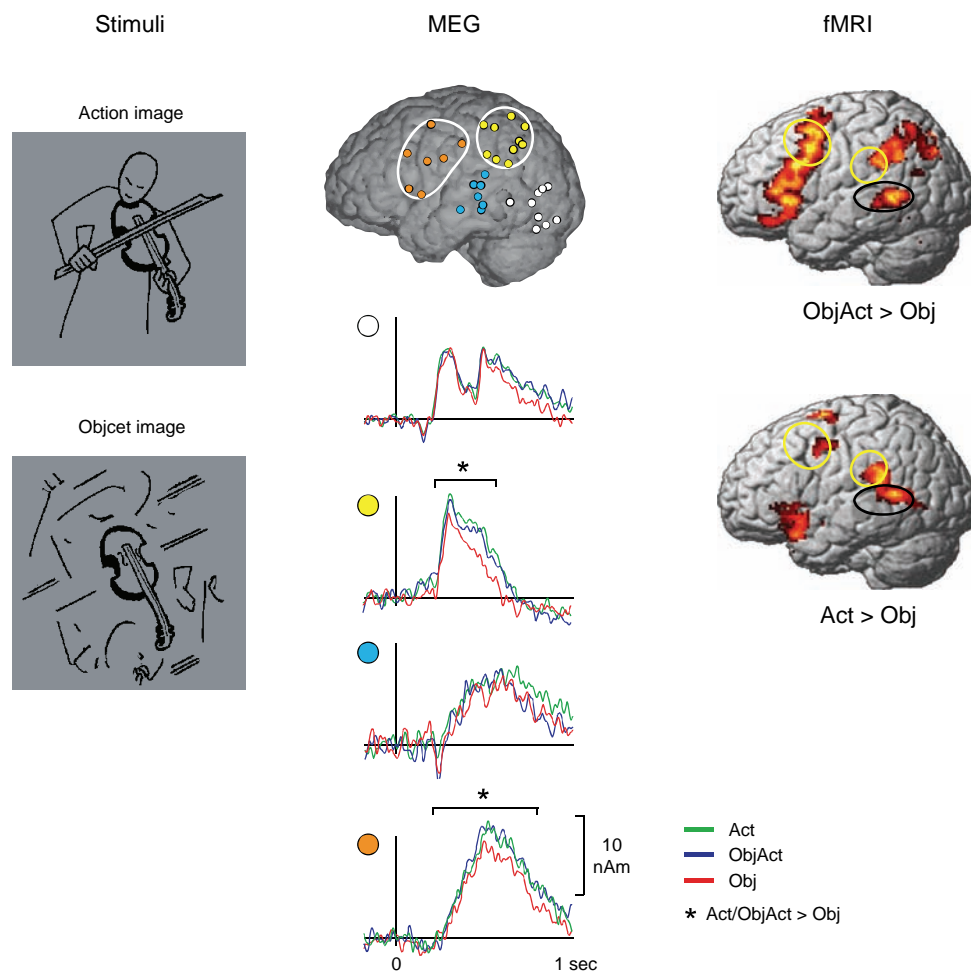


Figure 4. Main results of Study I. **Left:** Examples of the stimuli and the main results of Study I. **Middle:** MEG source clusters (top) and their respective time courses (below). **Right:** Main fMRI results. The MEG and fMRI results show that the same general pattern of activation was observed with both brain imaging methods. The main effect was also observed with both methods, namely that action images elicited greater activation than object images in the left frontal and parietal region (white ellipses, MEG; yellow ellipses, fMRI). Additionally, fMRI showed this effect also in the left posterior temporal cortex (black ellipses). For visualization purposes, the figure displays fMRI images uncorrected for multiple comparisons ($p < 0.001$)

In the MEG recording, the participants performed the task both overtly and covertly in separate runs. A behavioral evaluation of the naming latencies in the overt condition showed that participants were significantly slower at naming objects from action images than from object images⁵. The results are in agreement with those of Sörös et al (2003) who used many of the same action images that were included in this study. While verbs in general are named more slowly than nouns (Szekely et al., 2005), it seems that accessing the object from a picture that includes additional information demands additional cognitive effort. This observation can be seen as a further indication that the content of the image matters on several levels of processing.

Both the MEG and fMRI results of Study I indicate that verbs and nouns in healthy humans evoke a similar distributed network of brain activation in picture naming, but that the type of images used may have a pronounced effect on the neural activation in this network. This interpretation agrees with the conclusion of a recent review which argued that grammatical class is probably not an organizational principle of knowledge in the brain (Vigliocco, et al., 2010).

4.2. Study II: Learning new names and meanings

Vocabulary growth in the native tongue is a mundane experience even in adulthood; we frequently encounter new words that are effortlessly incorporated into the mental lexicon. This feature of human language illustrates the dynamic characteristics of the mental lexicon: in addition to maintaining information, new phonological or semantic information is easily integrated with existing lexical entries. In this study, the neural correlates of vocabulary growth were charted by comparing the spatiotemporal correlates of newly learned words with those of familiar words.

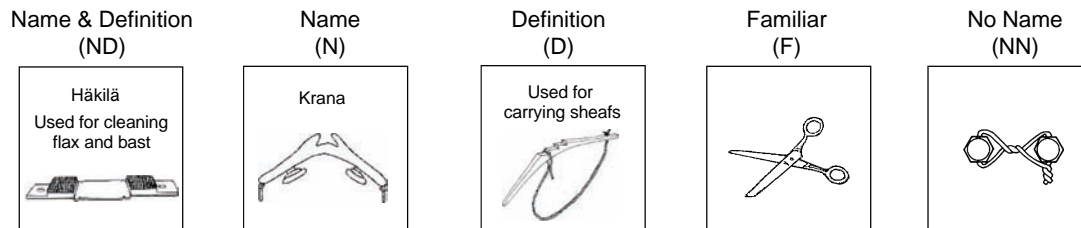
The participants performed a simple, delayed picture naming task during MEG recordings before and after behavioral training of novel words in the native language. To ensure equal activation of motor and articulatory planning for all conditions, the participants were instructed to say the generic word ‘object’ if they did not know the name or it did not come to mind. In order to specifically probe access to phonological or semantic information, two additional categorization tasks were performed on the second day after learning. Categorization of pictured items is similar to picture naming, but semantic categorization of an image may, in principle, be completed as soon as the item is recognized. Phonological categorization, on the other hand, should proceed until the phonological form is retrieved, before an evaluation of the name can take place (Humphreys, Price, & Riddoch, 1999; Indefrey & Levelt, 2004). In the phonological categorization task participants were asked to judge whether the name of the presented object started with the phoneme/letter “r”, whereas the semantic categorization required evaluation of the question “is this a fishing tool”. An overt response was required only for the target trials (3/3.5% of all trials in the phonological/semantic categorization task respectively), which were excluded from the analysis.

The main sequences of activation in the brain were very similar for both the naming and categorization tasks and agreed with previous picture naming and picture categorization studies (Levelt, Praamstra, Meyer, Helenius, & Salmelin, 1998; Salmelin, Hari,

⁵ ANOVA: $F(2,20) = 4.7$, $p < 0.05$, pair-wise comparison: $t(10)=2.7$, $p < 0.05$; these statistics were not reported in the original publication.

Lounasmaa, & Sams, 1994; Sörös, et al., 2003; Vihla, et al., 2006). In both tasks the activation proceeded from transient activation of the occipital cortex, through bilateral parietal activation (200-400 ms post stimulus) to more sustained activation of the left or bilateral temporal and frontal cortices (>300 ms). The main effect of learning was, in both tasks, observed in the left temporal cortex as a stronger neural response to items for which the participants had learned a name, compared to items for which no name information had been given (Figure 5). The effect was detected equally for items for which the participants only knew the name or knew both the name and the meaning. Phonological access in speech production has also previously been linked to activation

A. Stimuli



B. Picture naming

C. Picture categorization

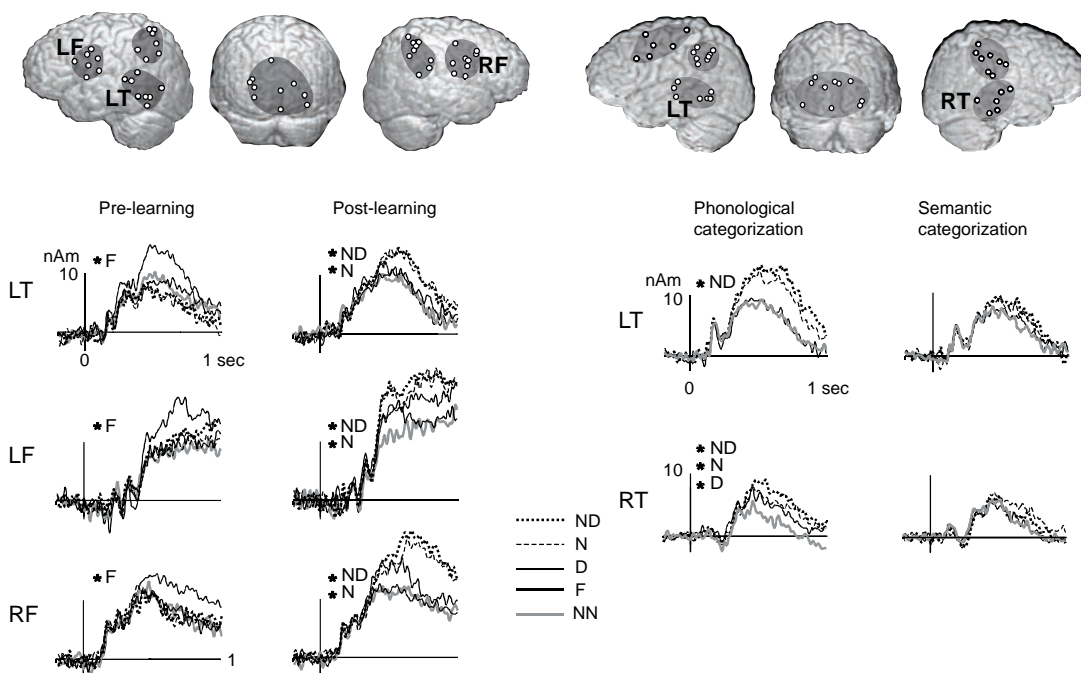


Figure 5. Main results of Study II. **A.** Examples of the stimuli as they were presented during training. In the MEG picture naming task, the pictures were presented without any written information. **B.** Source clusters in the picture naming task and the time course of activations in the regions showing learning effects: left temporal (LT), left frontal (LF) and right frontal (RF) cortex. Before learning, familiar items (F) elicited stronger activation than items with no name or definition (NN). After learning, activation to items with newly learned names (ND, N) was comparable to that evoked by the familiar items, and both also evoked stronger activation than the No Name items. **C.** Source clusters in the phonological and semantic categorization tasks. Time courses of activation are shown for the left (LT) and right (RT) temporal cortices. Significant effects were detected only in the phonological categorization task where items for which the participants knew the name (N, ND) elicited stronger activation in both the left and right hemisphere.

of the temporal cortex in the same time frame (250 ms onwards) (Indefrey & Levelt, 2004; Vihla, et al., 2006), as well as to increased phonological processing cost for accessing low-frequency words (Graves, Grabowski, Mehta, & Gordon, 2007).

In the picture naming task, phonological processing effects were also present in the bilateral frontal regions, but these areas did not show significant stimulus-specific effects in the phonological categorization task. The phonological categorization results suggest that phonological processing of newly learned items does not automatically proceed to post-lexical processing stages such as syllabification, but that this depends on whether articulation is required by the task. Phonological processing and motor preparation for articulation has also previously been linked to the frontal cortex (Bookheimer, 2002; Kuriki, Mori, & Hirata, 1999; Salmelin, et al., 1994; Vigneau, et al., 2006; Vihla, et al., 2006).

Access to the verbal definition of the tool use in the semantic categorization task did not evoke a specific neural referent for any of the stimulus categories. This may seem surprising as the task was designed to probe semantic processing, but several factors may account for the results. It is possible that some level of meaning was attached to all the stimuli during the learning phase, as they were all old tools and were learned in the same situation. Also, the picture itself may constitute some form of semantic referent, although the usage could not be visually determined from the images. If some level of semantic processing occurs for all object-like pictures, the present manipulation of the semantic information attached to the images may have evoked neural processing that was indistinguishable from that of the other stimulus categories. Even so, the clear effect of phonological processing and lack of clear-cut semantic effects seem to suggest that these two aspects of picture processing are subserved by different neural mechanisms.

In sum, the study showed that newly learned words can be incorporated into the mental repository of words and processed in a manner similar to familiar words. Furthermore, we showed that clear effects of phonological processing in picture naming and picture categorization are evident in the left temporal lobe. However, salient effects of semantic processing were lacking, despite being specifically targeted by a semantic categorization task. Thus, semantic and phonological information may be implemented and accessed in different ways in word production.

4.3. Study III: Maintaining new linguistic information

Only a handful of neuroimaging studies have investigated long-term memory that spans several days or months. Those studies that involve acquisition of new words have concentrated on learning-related changes rather than the maintenance mechanisms (Grönholm, et al., 2005; Raboyeau, et al., 2004). Conversely, the studies that incorporate both the encoding and retrieval phases have focused on episodic memory for arbitrary pairs of familiar words (Bosshardt, et al., 2005; Tulving, et al., 1994), but have not entailed acquisition of new linguistic information. The present study is the first attempt to track the neural correlates of long-term maintenance for newly learned words over several months. The study set off where the previous Study II ended, i.e., at the stage where all participants mastered all the novel words (Fully Learned stage). Participants from Study II were invited to the follow-up study to repeat the picture naming task after 1 week, 4 weeks, 2 months and 10 months. The performance in the

picture naming task was evaluated both from the online performance during the MEG scanning and offline with a paper-and-pencil test.

The brain activation sequence observed in the Fully Learned condition was reproduced in all post-learning recordings (see Study II). This included the prominent difference in the left temporal and frontal cortices between the learned items (Name, Name & Definition) and the unknown items (No Name) seen after learning in Study II. To facilitate comparison between different recording days, all conditions were baseline corrected to the level of activation evoked by Familiar items.

The behavioral evaluation showed that, in contrast to the relatively homogeneous training period, the number of forgotten words varied considerably between individuals, especially at the later recording points. However, at the 1-week checkpoint the behavioral performance was still close to the ceiling level (97.8 % correct), while considerable variation emerged in the neural responses. Interestingly, the changes in neural activation between the starting point and the 1-week recording successfully predicted the behavioral performance 10 months later (Figure 6). Individuals in whom the left frontal and temporal activation remained unchanged or increased generally performed well 10 months later, whereas decreased activation in the same areas implied poorer long-term naming performance. The two areas involved are well-known parts of both the memory and language networks of the brain. The left frontal cortex is suggested to play a role in phonological working memory and semantic memory retrieval, whereas the temporal lobe is suggested to subserve the declarative memory system (see, e.g., Cabeza & Nyberg, 2000a; Ullman, 2004). The two regions have also been linked to phonological and semantic processing in word production (Bookheimer, 2002; Indefrey & Levelt, 2004; Salmelin, et al., 1994; Vigneau, et al., 2006; Vihla, et al., 2006).

Previous studies have reported item-specific asymmetries between encoding and retrieval reflected by differential brain activity (Habib & Nyberg, 2008; Wagner et al., 1998) but the retention periods in these studies have been limited to less than one hour. Additionally these studies report effects related to the encoding or retrieval stage, rather than mechanisms underlying maintenance. In the present study the association between neural activation and behavioral long-term outcome was not item-specific, but instead seems to provide a neural measure on the individuals that successfully integrated the novel lexical entries as seemingly permanent representations in the lexicon. As both the encoding and retrieval performance were successful, the results may reflect part of the intermediate maintenance stage.

Automatic consolidation independent of active recollection or repetition, has been shown to be mediated e.g., by sleep (Davis, et al., 2009; Fenn, Nusbaum, & Margoliash, 2003) and it may also play a role in the present study. Another possibility is that the items entered a state of instability at the active recall one week later, during which the memory trace was either reinforced or weakened. Similar mechanisms have previously been demonstrated in animal models (Nader & Hardt, 2009). The present result may be an indication that such reconsolidation also occurs in humans at the system level and that memory maintenance is a dynamic process.

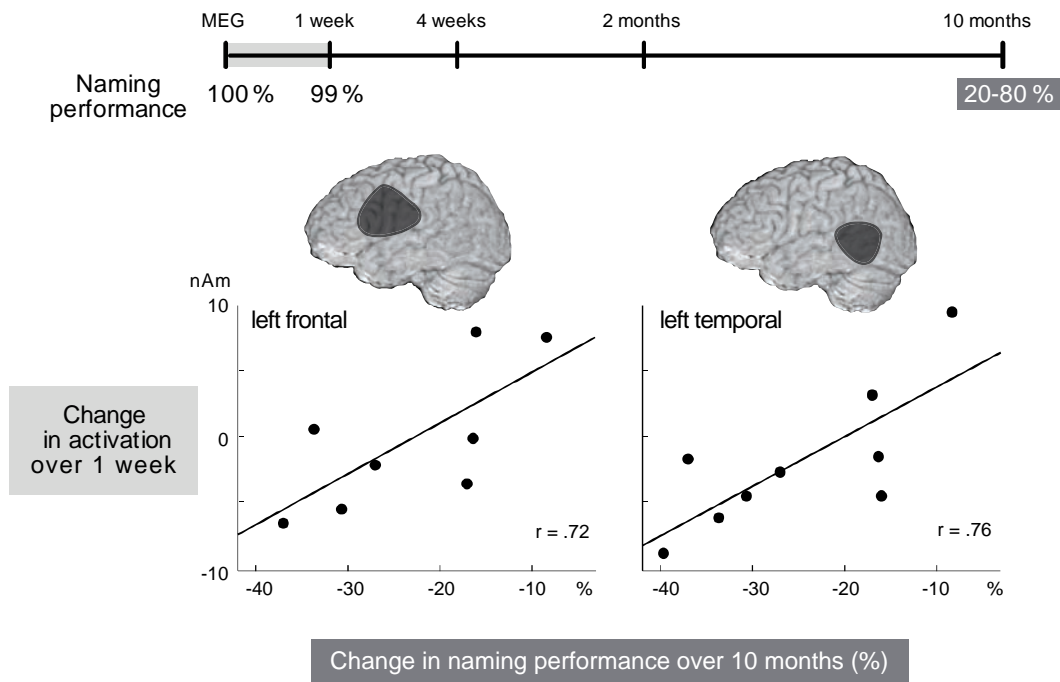


Figure 6. Correspondence between neural and behavioral measures of maintenance and forgetting.

4.4. Study IV: Sentence-level speech production with a newly learned miniature language

Studies I-III in this thesis focused on single-word processing. Study IV took one step further towards natural speech production and asked which cortical systems are involved in sentence-level processing. Producing sentences entails combining words according to a set of grammatical rules, but the way words and syntax are integrated on a neural level has remained unclear.

In this study, we specifically compared the planning and preparation for word output in the presence or absence of morphosyntactic constraints. In addition, the study aimed at investigating whether neural processing differs between the native and a newly learned language. Ten participants were trained for four days and then performed a two-stage picture-embedded cloze test task (Figure 7A). First, during the Picture only stage, a picture of two animals was presented and the participant was asked to think about the upcoming sentence or word sequence. In the sentence condition, the animal on the left was doing something to the animal on the right (e.g., kissing or begging); in the word sequence condition the animals were standing passively. Secondly, in the subsequent Cloze test stage, written words corresponding to the picture were superimposed on the screen one-by-one at 1.5 s intervals. Retrieval of the final word of the sentence or word sequence was signaled, instead of the written word, a string of question marks. The final word was produced overtly after a short (1.5 s) delay. The task was performed both in the native language (Finnish) and in the novel miniature language (Anigram), with the order counterbalanced across participants.

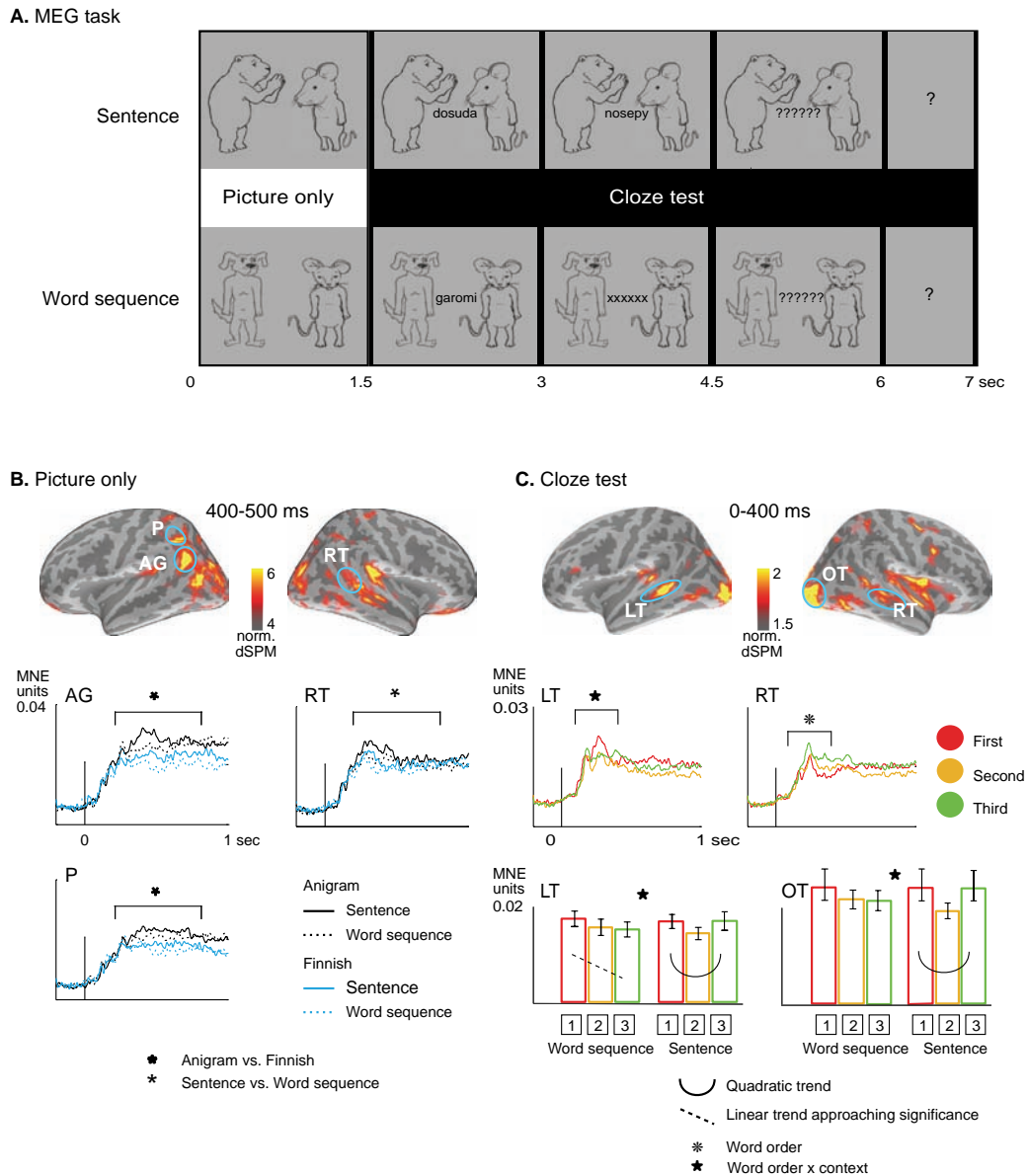


Figure 7. Main results of Study IV. A. Task design in the MEG recording. In the Picture only stage the participant was instructed to retrieve the names of the depicted objects and plan the upcoming sentence or word sequence. In the Cloze test stage, participants silently read each word, but covertly produced the final word of the sentence or word sequence, prompted by a string of question marks; the last, separate question mark was the cue for overt production of the final word. B. Main results for the Picture only part. Effects between the languages were seen in the left parietal cortex (P) and angular gyrus (AG); the main effect between sentences and word sequences was evident in the right temporal cortex (RT). C. The main results for the Cloze test. Decreased activation as a function of task progression appeared, among other regions, in the left temporal cortex (LT). The opposite effect, increased activation for task progression, was only observed in the right temporal cortex (RT). Activation increased selectively for the sentence-final object in the left temporal (LT) and right occipito-temporal (OT) cortex.

The Picture only stage can be seen as a phase, where each depicted word is retrieved from the lexicon and the upcoming sentence or word sequence is planned. Additionally the final word should be kept active in memory until the end of the task. Increased activation in the left temporo-parietal junction (angular gyrus) and the parietal area for Anigram than Finnish indicated that these processes were more taxing in the novel language (Figure 7B). Indeed, previous studies have also linked these areas to verbal working memory processing (Jonides, et al., 1998) and semantic concept retrieval (Binder, et al., 2009). The differences in neural processing between the two languages were limited to these effects during the Picture only stage.

In the Cloze test part, the progression of the task resulted in a decrease of activation for each presented letter string/word, which is typical of confirmed expectations (previously reported for e.g. word sequences in Vartiainen, Parviainen, et al., 2009). This effect was observed in a number of areas: the left temporal cortex (Figure 7C), temporo-parietal junction and supramarginal region, the right parietal cortex, and the bilaterally occipito-temporal cortex.

Right-hemisphere effects were seen in both the Picture only and the Cloze test part of the task. Planning of sentences and assignment of thematic roles to each depicted word in the Picture only stage was reflected by elevated sustained amplitudes in the right temporal cortex compared to word sequences. In the Cloze test, a somewhat more anterior part of the right temporal cortex showed increased activation with task progression (Figure 7C). Compared to the general effect of sequence progression this opposite trend in the right temporal cortex suggests a functionally different role. The right temporal cortex has previously been shown to be active in a cloze-type task on sentence-level production (Kircher, Brammer, Tous Andreu, Williams, & McGuire, 2001) and in combinatorial semantics (Graves, Binder, Desai, Conant, & Seidenberg, 2010). It may thus be that the right temporal cortex has a role in integrating combinatorial semantics in a syntactically structured context.

An effect for morphosyntactic processing in the form of increased activation to the sentence-final word was observed in the left middle temporal and right occipito-temporal cortex, between 100-400 ms after the written stimulus was presented (Figure 7C). In both languages, the covert production of the sentence-final object required the retrieval of the correct inflectional ending, which was not the case for the last word in the word sequence condition. In studies on language perception, inflectional morphology has been linked both to the left middle superior temporal cortex (Newman, Supalla, Hauser, Newport, & Bavelier, 2010; Vartiainen et al., 2009) and to the right occipito-temporal cortex (Zweig & Pylkkänen, 2009).

Frontal activation was observed for both languages and in all stages of the task, but did not distinguish between the conditions. Yet, previous fMRI and PET studies on speech production have often linked this area to sentence-level syntactic planning (Golestani, et al., 2006; Haller, Radue, Erb, Grodd, & Kircher, 2005; Indefrey et al., 2001). Differences in experimental baseline conditions may partly account for this discrepancy, but it may also be indicative of methodological differences between MEG and fMRI/PET (Study I in the present thesis; Vartiainen, Liljeström, Koskinen, Renvall, & Salmelin, 2011). In sum, the study showed that both the strain of a novel language and processing of grammatical structures affected the brain responses early on in the task. However, when the inflected word needed to be produced, the activation in the left

temporal and right occipito-temporal cortices was increased, indicating that additional effort was needed also at the time of production. The results further suggest functionally different roles for the left and right hemisphere in sentence production, with the left side involved in morphosyntax at the lexico-semantic level and the right side in combinatorial semantics.

4.5. Study V: Acquiring implicit knowledge of a novel phonology

Although learning foreign languages in adulthood often involves some type of formal and explicit learning, an important complementary source of knowledge is the incidental learning that is bound to co-occur with repeated exposure to a language. In relation to the proposed role of working memory and particularly the phonological loop, multiple exposures to a word should facilitate formation of a long-term representation (Baddeley, et al., 1998). At the level of the brain, repeated exposure to a word generally causes reduced neural activation (Grill-Spector, et al., 2006). This so-called repetition suppression effect occurs also for novel or unknown phonological forms (Graves, et al., 2008; Klein, et al., 2006; Majerus, et al., 2005; Moser, et al., 2009; Rauschecker, et al., 2008) and is generally seen as indicative of learning. The present study sought to determine whether this type of incidental learning differs between an unknown language (Korean) and the mother tongue (Finnish). From a language-learning perspective, it is also important to know to what extent the effects observed in short-term learning might transform into permanent memory representations. Sleep has been suggested to be one of the mediating mechanisms in the formation of long-term memory representations (Tamminen & Gaskell, 2008). Here long-term learning was estimated by evaluating the stability of learning-related neural modulation to the next day.

For each language (Korean and Finnish), two MEG measurements on consecutive days were performed for each participant, making a total of four measurements. On the first day, the participants heard and overtly repeated unknown Korean words or meaningless Finnish pseudowords that were presented either once (Nonrecurring) or five times (Recurring). The participants were not instructed to memorize or learn the words in any way but simply to repeat the words as accurately as possible after an auditory cue. On the second day, the task was identical, with the exception that both the Recurring and Nonrecurring words from the first day were presented only once and were mixed with 200 completely new items. If learning persists to the following day, any learning effects on Day 1 should be replicated on Day 2. The participants also performed a behavioral recognition task after the MEG recording, outside of the scanner. The same design was applied for both languages, in a counterbalanced order and with approximately one week between the different languages.

All learning effects were limited to the left hemisphere, although the general activation pattern was mostly bilateral. Repetition suppression similar to previous fMRI/PET studies on phonological learning (Graves, et al., 2008; Majerus, et al., 2005; Rauschecker, et al., 2008), was detected spatiotemporally separable horizontally (300-600 ms) and the vertically (600-1200 ms) directed sources in the superior temporal cortex (Figure 8). However, only in the vertical source cluster did the effect prevail to the next day in both languages, suggesting a more long-term type of learning. Also in behavioral test the Recurring words were better recognized than the Nonrecurring. The results show that implicit learning in the form of listening and repeating words can induce similar consolidation effects as those reported previously in a phoneme-

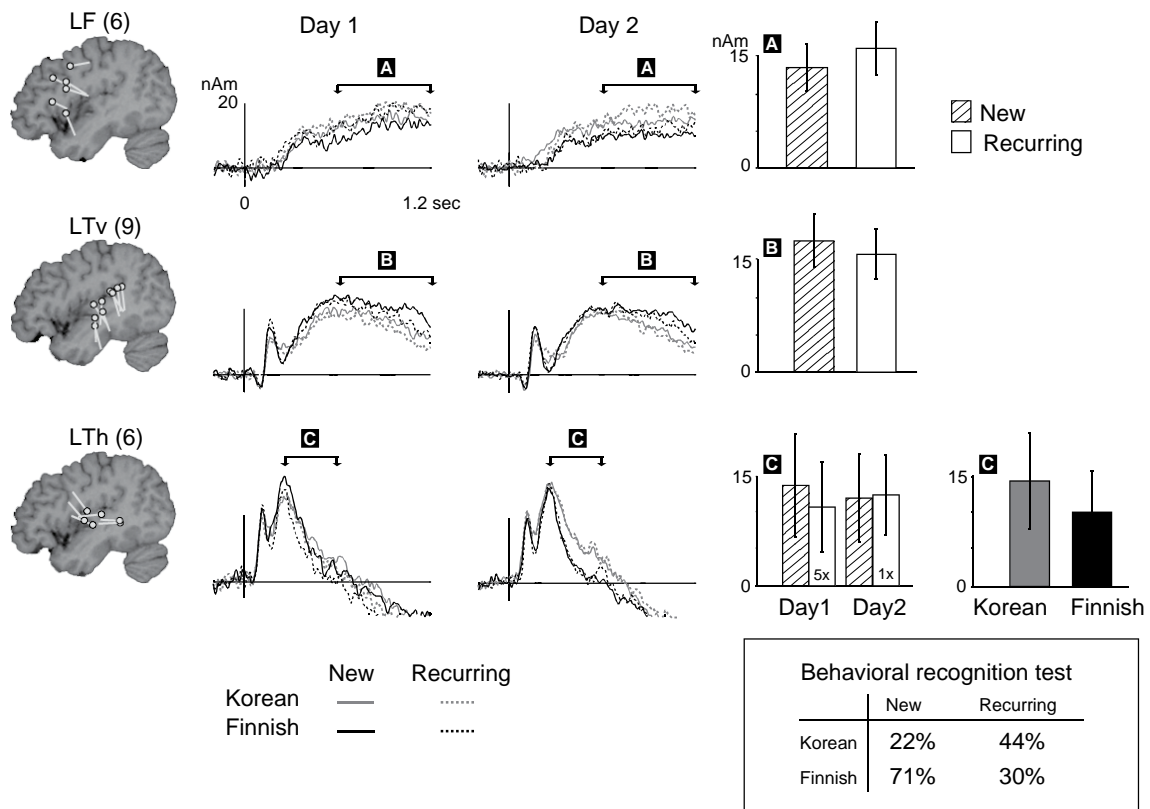


Figure 8 Main results of Study V. **Left:** Individual ECDs of each source clusters; left frontal (LF), left temporal vertical (LTV) and left temporal horizontal (LTh). **Middle:** The mean time course of activation in the source clusters on the two measurement days. Time windows with significant effects are marked with letters (A-C). **Right:** Main effects displayed as bar graphs; summary of the behavioral results.

monitoring task (Davis, et al., 2009). The learning is most likely related to learning of individual word forms rather than internalization of the novel phonotactic rules of Korean, as the effect was seen in both languages when only the Korean words entailed an unknown phonology.

Effects of long-term learning were also observed in the left frontal cortex, but in the form of increased activation to Recurring items. This is opposite to the effect reported in the temporal cortex in previous fMRI/PET studies (Klein, et al., 2006; Moser, et al., 2009; Rauschecker, et al., 2008). However, an important distinction is that the previous experiments used immediate production whereas the present Study employed delayed naming to avoid movement artifacts. Indeed, the observed effect is spatially and temporally similar to activation related to phonological planning and articulation as previously reported in MEG studies using delayed naming tasks (Study II in the present thesis; Vihla, et al., 2006). Thus, it is also possible that the observed effect is related to an increased effort of correctly pronouncing the Recurring words as they became more familiar.

An effect between the languages was observed in the horizontally oriented sources, which showed a stronger response to the novel Korean words than for the native Finnish pseudowords on both days. Increased activation in both hemodynamic and electrophysiological responses to a poorly mastered language are not uncommon (see, e.g. van Heuven & Dijkstra, 2010) and are usually interpreted as increased processing

demands, which also readily applies to the present results. The behavioral results give further support to this interpretation, as better recognition accuracy was detected for Finnish than Korean stimuli. The same region and time window (300-600 ms) also displayed learning that was more short-term. Repetition suppression was observed only for Day 1, although an overall shortening of the response was observed for all items on Day 2, including the new filler items. The results may be indicative of faster transition from perceptual processing to articulatory planning as the task became more familiar.

In sum, the left-hemisphere temporal and frontal cortex showed both short-term and long-term learning effects. The results suggest functionally and temporally distinct areas within the temporal cortex that can be separated primarily by their direction of neural current flow. The effect in the vertically oriented sources reflected more long-term learning, whereas the horizontally oriented sources were associated with short-term memory. Nevertheless, both languages activated the same set of cortical regions and displayed similar learning effects, suggesting that the learning reflected word-level representations rather than internalization of the new Korean phonology.

5. Discussion

The present thesis addressed the neurocognition of adult language learning and language processing in different linguistic domains, spanning from lexical processing to syntax. A particular emphasis was put on how these aspects are expressed in production which is, to date, notably underrepresented within the field of neuroscientific language research. The present thesis contributes to the field by describing neural correlates of phonological, semantic, and syntactic information in production of words and sentences.

A comparison between the present neuroimaging results and those reported in the contemporary literature on phonological, semantic, and syntactic processing, reveals both similarities and discrepancies when comparing modalities and tasks. In the left temporal cortex, the time course of activation is remarkably similar for auditory/visual word processing and picture naming, although there is variation in the more exact locations (Studies I-V; Dobel, et al., 2010; Vartiainen, Parviainen, et al., 2009; Vihla, et al., 2006). In written and spoken word perception, the sustained left temporal response is most often linked to lexical-semantic integration (Service, Helenius, et al., 2007; Vartiainen, Parviainen, et al., 2009). The same neural response pattern, is also involved in phonological processing, even in the absence of meaning (Study V; Bonte, Parviainen, Hytönen, & Salmelin, 2006; Kujala, Alho, Service, Ilmoniemi, & Connolly, 2004; Proverbio, Vecchi, & Zani, 2004; Simos et al., 2000). In the present studies on picture naming, phonological processing elicited strong modulations in the sustained temporal cortex response, irrespective of whether a verbal definition of the meaning was available (Study II). The left temporal cortex shows similar concurrent processing between different tasks also for syntactic information. In the picture-embedded sentence processing task in Study IV, activation in this area was clearly linked to processing of grammatical and morphosyntactic information. This functional role is in line with previous reports on temporal cortex activation in both language production and the perception (Haller, et al., 2005; Newman, et al., 2010; Service, Helenius, et al., 2007; Vartiainen, Aggujaro, et al., 2009).

However, with respect to semantic processing the story is more convoluted. In the present thesis, the temporal cortex was active in the two picture naming Studies (I and II) but did not show sensitivity specifically when accessing meaning (Study II). Nonetheless, imaging studies on lexical-semantic processing with receptive lexical tasks have repeatedly found activation of the left temporal cortex both in the spoken and written domain (Halgren et al., 2002; Helenius, et al., 1998; Maess, et al., 2002; Price, 2010; Service, Helenius, et al., 2007; Vartiainen, Parviainen, et al., 2009; Vigneau, et al., 2006). Thus, semantic access seems to be neurally dissimilar in picture naming and in perception of visual/auditory words. A picture needs to be identified before the name can be retrieved or categorized for content, whereas access to the meaning of a spoken or written word is preceded by initial processing of the form (Glaser, 1992). It is possible that the analysis of surface features of words and pictures differs in the way semantic access is achieved (for different views on initial processing within each modality see, e.g., Grill-Spector & Kanwisher, 2005; Harley, 2001). As discussed in Study II, several factors may contribute to the fact that the neural signatures of semantic access were hard to detect in picture naming or categorization. Firstly, processing of meaning might not be as time-locked in production as it is in perception, and second,

pictures may in themselves elicit semantic processing that could mask the subtle distinctions in meaning needed for a semantic categorization task.

The observed similarities and differences between word recognition and picture naming give rise to a further issue. First, albeit these tasks do not provide full descriptions of perception or production, the comparison shows that the input and output systems should not be reduced to mirror-images of each other. Moreover, these differences and similarities call for more research especially within the field of sentence-level speech production, which is extremely underrepresented compared to sentence-level comprehension. Secondly, the spatiotemporal brain activation patterns of both domains may give valuable information on how phonology, semantics, and syntax interact in the mental lexicon. A fruitful approach towards a more complete neural description of the mental lexicon might be to study phonological, semantic and grammatical information processing across the input and output domains.

The role of grammatical information in the organization of the mental lexicon has been a subject of a long-standing debate (for a review see, e.g., Vigliocco, et al., 2010). The results of noun and verb processing in Study I contribute to this debate by showing that in picture naming the type of the image used seems to be more relevant than the grammatical class of the word that needs to be produced. This finding has also clinical implications, as the types of images used to assess category-specific impairments of aphasic patients may affect their performance. In Study I, the same main effects of action versus object naming were observed both with MEG and fMRI. However, a recent study comparing fMRI and MEG results in reading found both functionally and spatially divergent results between the two methods when comparing letter-strings to symbols or noise-embedded words (Vartiainen, et al., 2011). As discussed by Vartiainen and colleagues, it is possible that the hemodynamic and electrophysiological signals are differently sensitive to top-down and bottom-up processing. If this turns out to be a systematic pattern, the two imaging methods may give very useful complementary information that should be taken into account in neuroscientific language research.

In Study IV, the sentence-level processing of grammatical and morphosyntactical aspects was reflected as increased activation in the right and left temporal cortices, respectively. This may well be related to the suggested broader and more overlapping word representations in the right hemisphere compared to the left hemisphere (Jung-Beeman, 2005). As sentence-level combinatorial semantics necessarily involve grammar and syntax, the proposed role for the right hemisphere might be particularly relevant. Future studies may further clarify the extent to which the two hemispheres contribute to complementary forms of language processing.

Three models of word/language learning that were presented in more detail in the Introduction, namely the CLS (Davis & Gaskell, 2009), the working memory (Baddeley, et al., 1998) and the declarative/procedural model (Ullman, 2001a, 2001b). The studies in the present thesis were not explicitly designed to test these models, but the models nevertheless have important bearings on the studies in the thesis. Building on the CLS model, over-night retention periods were used in all the language learning experiments included in the present thesis (Studies II-V). In line with the hypothesized second stage of the CLS model, Studies II-III show that cortical markers of consolidated word representations can be attained by a straightforward picture naming task in MEG.

Both multiple word exposure and overt rehearsal have been linked to phonological working memory functions when learning words in a new language (Ellis & Beaton, 1993; Papagno, Valentine, & Baddeley, 1991). In Study V this type of phonological learning was combined with over-night consolidation in line with the CLS model. The results showed that learning-related modulations in neural activity were induced both on the day of the learning and the next day in temporal areas that have previously been linked to both phonological processing (Bonte, et al., 2006) and active short-term maintenance (McGettigan, et al., 2010). However, the temporal cortex activation could be divided into two functionally distinct areas; the vertically directed sources maintained the learning effects to the next day, whereas the horizontally directed sources only showed learning effects during the learning phase. Such a neural division of labor would seem to agree with the CLS model, which predicts separation of the immediate learning effect and long-term consolidation; short-term echoic processing is included in both the working memory model and CLS. Whether the observed immediate learning effect was mediated also by medial regions (as specifically predicted by the CLS) remains a topic for further research; neural activity in deeper areas such as the hippocampus is not readily detected with MEG.

The declarative/procedural model (Ullman, 2001a, 2001b) makes the specific prediction that first and second language processing differs in their respective recruitment of the two memory systems. Accordingly, different brain regions should dominate in these two languages. Still, in Study IV which contrasted novel and native language processing, no neural differences were found in the way grammatical information was processed in the two languages. Indeed, the differences seen between the languages are more likely to reflect increased demands on working memory and word retrieval due to a lower proficiency in the novel language. In effect, Study IV did not offer any evidence for qualitative differences between grammatical and lexical information, not even in the mother tongue. Instead, the phonological loop described in the working memory model seems to provide a more appropriate account to the task that was used. Planning an upcoming sentence or word sequence is akin to the word span task commonly used to assess the phonological loop (Baddeley, et al., 1998). In line with this interpretation, the increased activation of the left parietal cortex and angular gyrus also coincided with the postulated cortical locus for this type of task (Baddeley, et al., 1998; Buchsbaum & D'Esposito, 2008).

Applying a functional description of memory to language learning should entail specific descriptions for all three stages: encoding, maintenance, and retrieval. Previous studies have shown that neural measures of successful encoding predict successful retrieval (Bosshardt, et al., 2005; Wagner, et al., 1998). In the combined results of Studies II and III both the acquisition, maintenance and retrieval phase of word learning were examined, although no neural measures were collected during the actual encoding phase. The results of these studies showed that newly learned and familiar words were processed in a similar way, suggesting that the newly learned words had been integrated into the mental lexicon. Reconsolidation, i.e. the strengthening or weakening of memory traces during retrieval, as one form of memory maintenance (Nadel, 2007). In Study III, the neural activation in the left temporal and frontal cortices one week after learning may be related to this kind of maintenance. Intriguingly, at a time when naming of the newly learned words was still virtually flawless, the change in neural activation was nevertheless predictive of the ten-month stability of the new vocabulary in an individual. While one cannot completely disregard that the differences might, in part,

stem from the encoding stage, all participants exhibited successful encoding as the training continued until they mastered the new words. The reason why the reconsolidation was successful in some participants but not in others remains, nevertheless, an open question. The participants were all university-level students/graduates and showed a high digit span, which should promote good language learning (Service, Maury, & Luotonen, 2007). Moreover, the baseline correction of the MEG response to the familiar items in each session presumably canceled out any major sources of random variability between the measurement days. Thus, the most obvious sources of external variations could be ruled out, suggesting that the underlying effect is probably related to subtle individual differences.

Studies IV and V examined language learning by comparing processing a foreign (or artificial) language to the mother tongue. The same cortical regions were active both for foreign and native language processing. However, the brain responses indicated increased processing effort in both the Anigram and Korean language compared to the mother tongue. Listening to Korean words compared to native language pseudowords increased the activation in the left superior temporal cortex, whereas planning an upcoming sentence or word sequences in the miniature language showed increased activation in the angular gyrus and the parietal cortex. The observed pattern is concurrent with the one suggested by Abutalebi (2008), in that non-native-like proficiency in a second language will either increase the activation in language processing areas (such as the superior temporal gyrus) or in areas for general cognitive control (such as the prefrontal or parietal cortex). It also highlights the different task demands in the two studies. Listening to Korean words entailed no explicit memory task, whereas producing sentences or word sequences in Anigram required explicit retrieval of the previously learned miniature language.

Studies on bilingualism tend to make a distinction between early and late language learning, often referring to the critical or sensitive period hypothesis and the changes of plasticity that occur early on in the development (Perani & Abutalebi, 2005). Still, other mechanisms of learning such as long-term potentiation are thought to be present throughout the life span. Also, the basic functional stages of encoding, maintenance and retrieval apply to adults and children alike. The present results show that these mechanisms are sufficient for native vocabulary growth and for novel language learning, albeit proficiency in a new language would be limited. However, it still remains open to what extent different types of linguistic information (e.g., grammar or phonology) are represented and accessed differently at different ages. Another unresolved general issue is whether acquisition of linguistic information is different from acquisition of other types of information. Although these questions lie beyond the scope of the present thesis, they provide important future directions for neurocognitive research on language processing and language learning.

6. Conclusions

The present thesis focused on the neural correlates of adult language learning and language processing. While it addresses several theoretical and methodological issues in this research area, its main focus is on the relatively little studied field of adult language learning. The results show that while anatomically distinct brain areas are engaged in learning new words, grammar and phonotactic rules, these areas are also employed by the same tasks in the native language. Activity levels in these networks are modulated by language proficiency levels, showing evidence for greater load when processing newly learned linguistic materials as compared to the native tongue.

The studies in this thesis may help in understanding how language is organized in the brain. In native vocabulary growth, new words can be integrated in the mental lexicon, reflected by similar behavioral and neural measures for new and familiar words. A particularly novel finding relates to the predictive value of neural responses following successful word learning. This effect may reflect system-level reconsolidation of memory traces in humans. It deserves to be studied further also because it appears to provide a marker for the large interindividual differences in long-term word learning. Relating language learning to memory mechanisms, as attempted in the present thesis, should help in bridging the gap between the long-separated fields of language and memory research.

Let us return to the Introduction and the case of Helen Keller who, with time, became a well-known scholar and writer despite the linguistic challenges she had to confront early in her life. She later described the language-learning experience in a way that could also easily be used to describe the studies in the present thesis:

“Gradually from naming an object we advance step by step until we have traversed the vast distance between our first stammered syllable and the sweep of thought in a line of Shakespeare.”

(Keller, 1903)

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ISBN 978-952-12-2541-3