

# **RAPID FORMATION AND ACTIVATION OF LEXICAL MEMORY TRACES IN HUMAN NEOCORTEX**

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# ABSTRACT

Rapid learning of new words is crucial for language acquisition, and frequent exposure to spoken words is a key factor for the development of vocabulary. More frequently occurring (and thus more familiar) words can, in turn, be expected to have stronger memory representations than less frequent words. The neural mechanisms underlying these representations are, however, largely obscure. Even less is known about the mechanisms related to the initial acquisition of new word-forms and build-up of lexical representations. The current thesis investigated how the neural traces are activated when known and novel spoken words are perceived, and how they can be formed when novel words are first encountered and repeated. The neural processes of word memory-trace activation and rapid formation were studied in adults and children using event-related potentials.

In adults, words with high frequency of occurrence elicited greater neural responses than low frequency words or meaningless pseudo-words already at ~120 ms after the time when they could be identified. Higher frequency words activated predominantly left frontal and anterior temporal cortices while the low frequency and pseudo-words showed a more bilateral temporal cortex activity. Neural dynamics during brief exposure to novel word-forms showed a rapid response increase at ~50 ms. This enhancement was associated with behaviourally-established memory performance on the novel words, confirming the relation of this neural dynamics to word learning. The enhancement, originating in the left inferior frontal and posterior temporal cortical sources, was specific to phonologically native word-forms and, furthermore, independent of whether the spoken sounds were ignored or attended to, suggesting a high degree of automaticity in native word-form acquisition. For novel word-forms with non-native phonology, such a response enhancement was not significant, while the response to known words attenuated over exposure, likely reflecting repetition-related suppression.

Furthermore, individual language experience influenced the neural learning dynamics such that greater number of previously acquired non-native languages with earlier average age of acquisition predicted larger response enhancement to novel non-native word-forms whereas later average age of acquisition predicted greater increase

to attended novel native words. Finally, a rapid response increase to an ignored novel native word-form in brief exposure was also observed in school-age children, and was underpinned predominantly by left prefrontal cortex and associated with writing accuracy. Remarkably, children with dyslexia failed to show such neural dynamics, suggesting deficient mechanism for automatic spoken word acquisition in dyslexia, a finding potentially relevant for further clinical research. In sum, the results suggest that exposure is key in defining the strength of perisylvian memory traces for words that can be formed rapidly and automatically in adults and typically developing children.

# TIIVISTELMÄ

Uusien sanojen nopea oppiminen on ratkaisevan tärkeää kielenoppimisessa ja toistuva altistuminen puhutuille sanoille on keskeistä sanavaraston kehittymisen kannalta. Toistuvammin esiintyvien (ja näin ollen tutumpien) sanojen muistiedustumien oletetaan olevan vahvempia verrattuna harvemmin esiintyvien sanojen edustumiin. Näiden edustumien taustalla olevat hermostolliset mekanismit ovat kuitenkin laajalti tuntemattomat. Vielä vähemmän tiedetään mekanismeista, jotka liittyvät uusien sanahahmojen oppimisen alkuvaiheisiin ja edustumien muodostumiseen osaksi sanastoa. Tässä väitöskirjassa selvitettiin, miten muistijäljet aivoissa aktivoituvat havaittaessa tuttuja ja uusia puhuttuja sanoja, sekä miten muistijäljet muodostuvat uusia sanoja ensi kertaa ja sen jälkeen toistuvasti kuultaessa. Muistijälkien aktivoitumisen ja nopean muodostumisen hermostollista perustaa tutkittiin aikuisilla ja lapsilla rekisteröimällä tapahtumasidonnoisia jännitevasteita.

Tulokset osoittavat, että aikuisilla sanat, joilla oli korkeampi esiintymistaajuus, saivat aikaan suuremman aiovasteen kuin matalamman esiintymistaajuuden sanat tai merkityksettömät epäsanat. Vaste esiintyi jo ~120 ms sanan tunnistusajankohdan jälkeen. Korkeamman esiintymistaajuuden sanat aktivoivat pääasiallisesti vasemman otsalohkon ja etummaisena ohimolohkon aivokuoria, kun taas matalan taajuuden sanoille ja epäsanalle syntyneet vasteet havaittiin ohimolohkojen aivokuorella pään molemmin puolin. Lyhyt altistuminen uusille sanoille sai aikaan nopean aiovasteen kasvun. Tämä kasvu oli yhteydessä uusien sanojen mieleenpalauttamiseen ja tunnistamiseen altistuksen jälkeen, mikä vahvisti käsitystä, että aiovasteessa tapahtunut muutos liittyi sanojen oppimiseen. Vasteen kasvu oli peräisin vasemman aivopuoliskon alemman otsalohkon ja taemman ohimolohkon aivokuorilta. Se oli merkitsevä vain äidinkieliä sisältäville uusille sanoille ja esiintyi huolimatta siitä, kohdistettiinkö tarkkaavaisuus sanoihin vai ei, viitaten äidinkielisten sanojen oppimisen olevan pitkälti automaattista. Vieraita äänneitä sisältäville sanoille syntyneessä vasteessa ei tapahtunut merkitsevää kasvua ja ennestään tutuille sanoille syntynyt vaste heikentyi altistumisen seurauksena todennäköisesti toistamiseen liittyvän suppression johdosta.

Lisäksi kokemus kielten oppimisesta vaikutti neuraalisen oppimisen yksilölliseen vaihteluun siten, että aiemmin opeteltujen vieraiden kielten suurempi määrä yhdistettynä keskimäärin aikaisempaan aloitusikään oli yhteydessä suurempaan aivovasteen kasvuun uusille vierasperäisille sanoille. Myöhäisempi aloitusikä sen sijaan ennusti suurempaa kasvua uusille äidinkielisille sanoille. Myös kouluikäisillä lapsilla lyhyt altistuminen uusille äidinkielisille sanoille johti aivovasteen kasvamiseen. Vasteen kasvun perusta oli pääosin vasemman etuotsalohkon aivokuorella ja se oli yhteydessä kirjoitustarkkuuteen. Sen sijaan lapsilla, joilla oli lukihäiriö, ei tapahtunut vastaavanlaista vasteen kasvua viitaten puutteelliseen sanojen oppimisen aivomekanismiin lukihäiriössä. Tulosten perusteella olennaista sanojen neuraalisten muistijälkien vahvuudelle on niille altistuminen, minkä avulla muistijäljet voivat muodostua nopeasti ja automaattisesti aikuisilla ja tyypillisesti kehittyvillä lapsilla.

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*Lilli Kimppa*

# LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications which are referred to in the text by their roman numerals.

- I Shtyrov, Y., Kimppa, L., Pulvermüller, F., & Kujala, T. (2011). Event-related potentials reflecting the frequency of unattended spoken words: A neuronal index of connection strength in lexical memory circuits? *Neuroimage*, *55*(2), 658–668.
- II Kimppa, L., Kujala, T., Leminen, A., Vainio, M., & Shtyrov, Y. (2015). Rapid and automatic speech-specific learning mechanism in human neocortex. *Neuroimage*, *118*, 282–291.
- III Kimppa, L., Kujala, T., & Shtyrov, Y. (2016). Individual language experience modulates rapid formation of cortical memory circuits for novel words. *Scientific Reports*, *6*, 30227.
- IV Kimppa, L., Shtyrov, Y., Partanen, E., & Kujala, T. (Submitted). Impaired online word learning mechanism in the dyslexic brain.

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# ABBREVIATIONS

ANOVA	analysis of variance
AoA	age of acquisition
BA	Broadmann area
DLPFC	dorsolateral prefrontal cortex
DP	word divergence point
EEG	electroencephalography
EOG	electro-oculogram
ERP	event-related potential
IFG	inferior frontal gyrus
IQ	intelligence quotient
LIFG	left inferior frontal gyrus
LORETA	low resolution brain electromagnetic tomography
MNE	minimum-norm estimate
MRI	magnetic resonance image
MTG	middle temporal gyrus
n.s.	non-significant
RAN	rapid automatized naming
RAS	rapid automatized switching
rmANOVA	repeated measures analysis of variance
ROI	region of interest
SD	standard deviation
SEM	standard error of mean
SOA	stimulus onset asynchrony
STM	short-term memory
STG	superior temporal gyrus

# 1 INTRODUCTION

The ability to rapidly acquire and the capacity to retain and recognise tens of thousands of words is a unique feature of human cognition that enables abundant and effortless sharing of information. Across the lifespan, an individual is exposed to an enormous number of native as well as non-native words, primarily by way of speech perception. Exposure to a single word can be short-lived or recurring, frequent or rare. Largely dictated by the frequency of such exposure to specific words, the mental lexicon, or vocabulary, is formed and extended.

This thesis explores the neural correlates of exposure-related properties of spoken word recognition in healthy adults and children, as well as in children with dyslexia. The studies focus on the phonological aspect of words, i.e. the word-form that, even without any semantic connotations, distinguishes spoken language from other utterances and sounds.

## 1.1 SPOKEN WORD RECOGNITION

In order to discuss the processing of words, it is necessary to define the term. Generally a ‘word’ refers to a language unit that is constructed of one or more syllables, which embed phonemes, the smallest components of language that distinguish a word from another. Crucially, a ‘word’ usually refers specifically to *known* words, as in those that are known in the language and are part of the lexicon. In other words, we have memory of the words used in our own communication. Furthermore, a word has a meaning, a semantic association to an object, action, or abstraction. Long-term memory for and semantics of words are the critical aspects that distinguish them from pseudo-words, i.e. words that could be phonologically and phonotactically well-formed words of the specific language in question but do not have a meaning nor belong to the lexicon. This distinction between known words and pseudo-words is referred to as the ‘lexical status’ or ‘lexicality’ of the word-form.

The recognition of spoken words relies on the extraction of distinct phonological word-forms from the auditory speech signal. After the initial stages of subcortical processing, the speech signal passes to the core auditory cortex (Heschl’s gyrus) and

then to the adjacent posterior superior temporal cortex (Scott & Johnsrude, 2003; Obleser et al., 2007), followed by processing in other areas of the left-dominant perisylvian language cortex (Catani et al., 2005; Price, 2010; Turken & Dronkers, 2011). The areas involved specifically in lexical processing (i.e. processing of known words as opposed to non-lexical pseudo word-forms) were found to include the posterior middle and inferior temporal gyri (MTG and ITG, respectively), inferior parietal lobe, angular gyrus, supramarginal gyrus, the anterior temporal cortex, and inferior frontal gyrus (IFG) of the left hemisphere (e.g. Démonet et al., 1992; Binder et al., 2000; Davis & Gaskell, 2009; Kotz et al., 2010). Such wide-spread activation indicates that access to words in the brain is dependent on a distributed left-lateralised fronto-temporo-parietal system that processes the acoustic-phonetic lexico-semantic input (Tyler & Marslen-Wilson, 2008).

Several psycholinguistic models of speech perception describe the recognition process of spoken words. These theories aim at explaining how the dynamic temporally unfolding speech signal is analysed from the early phase of acoustic-phonetic identification to the final recognition of the correct word. The Cohort model (Marslen-Wilson, 1987) defines a context-independent bottom-up model of word-form access and selection. According to the model, a cohort of words that transiently match the initial phonetic make-up of the perceived sensory input within the course of the temporal unfolding of the spoken word is accessed and activated. Initially the activation for all possible word candidates, or ‘competitors’, is high. As more of the speech signal unfolds, the activation levels of the mismatching competitors decline, whereas the activation level of the correct word rises and it is selected in the mental lexicon. This model thus suggests ‘online’ parallel activation of multiple items and processes. The TRACE model (McClelland & Elman, 1986), on the other hand, describes an interactive activation process where each temporally unravelling phoneme activates possible words in the lexicon and at the same time inhibits those that no longer remain possible candidates. Thus the temporal activation pattern of the competing words according to TRACE is distinctly different from that produced by the Cohort model in that the activation levels for the possible word candidates are initially low and gradually modulated by the excitatory input from each time-step to the next, with inhibition of mismatching competitors at each step. In other words, the

activation level of each time-step is dependent of the prevailing inhibition and the proceeding excitation, but also of the activation level of the previous step.

The density and structure of the mental lexicon, i.e. all available words in memory, are believed to form a crucial context to spoken word recognition process in the Neighbourhood activation model (Luce & Pisoni, 1998). This model not only considers the phonetic input to stimulate the competition of word representations but also to interact with the phonetic-phonological structure and frequency of the competitors. This makes the lexical access and activation reliant on the number of phonological neighbours and their probability in the language. Phonotactic probability, for example, defines the odds for certain phonetic segments to follow each other and this knowledge is acquired by experience. Distributed cohort model (Gaskell & Marslen-Wilson, 1997), however, rejects the role of phonological neighbours as critical in lexical access. Instead, the distributed model proposes direct mapping of the acoustic-phonetic input onto the available connectionist network of word representations. This model does not include any intermediate analysis stages, such that are present in TRACE, but enables partial network activation when the low-level acoustic-phonetic input is not sufficient to activate the total network of a specific word, unlike in Cohort model. Meaning of the word, i.e. semantics, is accessed simultaneously with the lexical form. Ultimately, in order for such distributed networks to exist, learning through experience is required.

Experience of different words is achieved through encounters. Indeed, processing of spoken words is closely intertwined with their frequency of occurrence in the language. Behaviourally, this was shown early on: Words with higher frequency of occurrence were processed more quickly than words with low frequency (Howes & Solomon, 1951; Broadbent, 1967; Morton, 1969). Experimental behavioural research was, however, unsuccessful in determining whether the frequency effect takes place early in the word recognition process (Marslen-Wilson, 1990; Rudell, 1999; Dahan et al., 2001), approximately at the time as lexical access, or at a later decision-making stage, i.e. post-access (Connine et al., 1993; Morrison & Ellis, 1995). Neuroimaging studies of visual word recognition indicate relatively early effects of frequency at 110-190 ms after stimulus onset (Serenio et al., 1998, 2003; Assadollahi & Pulvermüller, 2001, 2003; Hauk & Pulvermüller, 2004; Hauk et al., 2006; Penolazzi et al., 2007). The perception of visually presented words in which the complete word-form is

instantly available is, however, different to that of spoken words that provide temporally gradual input. Research on the neural processing of words with differing frequencies presented in the auditory modality is lacking.

## **1.2 MEMORY TRACES FOR WORDS IN THE BRAIN**

To explain and investigate lexical representations and their activation in the brain, a neurobiological model of language is required as a basis for hypotheses and testing. One such theory stems from a connectionist model of associative neural learning (Hebb, 1949). According to the model, words are represented in connected cell assemblies that are distributed across the cortex, with a focus on left-lateralised perisylvian regions (Pulvermüller, 1999). Such distributed networks for words are established with experience (Garagnani et al., 2007), through perception of spoken stimuli which prompts neural firing. The co-activation of a set of neurons in recurrent exposure to a word supposedly leads to the synaptic strengthening of internal connections between the participating neurons according to Hebbian learning rules (Hebb, 1949; Pulvermüller, 1999). The resulting ‘cell assembly’ (Pulvermüller, 1999) or ‘engram’ (Hebb, 1949) is often referred to as a memory trace. The memory trace is activated whenever the cells of the assembly fire in response to matching sensory stimulation. The model proposes that linguistic properties of the word, such as semantics, are part of the network, and thus these properties are accessed near-simultaneously with the phonological form.

The neural representations for spoken words have been studied using hemodynamic neuroimaging methods such as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), as well as with electrophysiological measures (electro- and magnetoencephalography EEG and MEG, respectively). Determining the differences in the neural processing of known words with presumed long-term memory-traces as opposed to pseudo-words with no pre-existing memory circuits, exhibits retrospectively how memory and possibly other features (such as acquired semantics) may have shaped the word representations in the brain.

Studies measuring hemodynamic brain responses during tasks involving perception of spoken stimuli have shown variable patterns of neural activation to words and pseudo-words. During phoneme monitoring tasks, pseudo-words were

found to activate the bilateral posterior superior temporal gyrus (STG), left inferior parietal lobe (IPL) and right IFG more than known words (Newman & Twieg, 2001). A lexicality effect during primed lexical decision task showed more activation for pseudo-words in left anterior and middle STG as well as the right middle frontal gyrus, and conversely for words in bilateral posterior MTG and IPL regions (Kotz et al., 2002). In contrast to this result, observed higher levels of activation related to lexico-semantic compared to phonological processing were observed in temporal, parietal and frontal association areas (Démonet et al., 1992). Passive listening to spoken words compared to pseudo-words showed greater activation in left posterior temporal areas (Shtyrov et al., 2008) and in some cases additionally in LIFG (Price et al., 1996; Friederici et al., 2000). However, some studies without an overt task on the spoken stimuli showed no differences in the bilaterally emerged activation of STG between the stimulus types (Wise et al., 1991; Binder et al., 2000). And finally, some studies reported overall greater responses to known spoken words over pseudo-words (Orfanidou et al., 2006).

These considerable differences in the found activations most probably stem from the use of different kinds of tasks that create different cognitive demands on processing the stimuli (cf. Kuperberg et al., 2008). Furthermore, with the poor temporal resolution of hemodynamic responses, it is not possible to infer from which stage of the lexical analysis the observed activations derive. For these reasons, employing methods with finer-grained temporal scale and paradigms controlling the cognitive processing requirements between conditions is essential.

### **1.2.1 EVENT-RELATED POTENTIALS AS A MEASURE OF WORD MEMORY-TRACE ACTIVATION**

Event-related potentials (ERP) are voltages reflecting the electrical activity of the brain, measured with electrodes placed on the scalp and extracted from continuous EEG (Luck, 2012). An ERP is time-locked to an event, such as a spoken stimulus, and its amplitude and latency indicate the sum of postsynaptic potential responses of primarily cortical pyramidal, but also subcortical, neuron populations to the event (Bressler & Ding, 2006; Luck, 2012). The amplitude, latency and topographical



distribution of ERPs can be modified by changes in physical stimulus features as well as by cognitive processes such as attention (Näätänen & Winkler, 1999).

The significant advantage of ERPs over hemodynamic neuroimaging methods is the millisecond temporal resolution with which the response pattern relative to specific time points can be analysed. In the investigation of neural processing of spoken words this is of high importance since the acoustic speech signal reaches the primary auditory cortex from the cochlea via the brainstem and midbrain extremely rapidly, in only ~20 ms (Rupp et al., 2002), which can then transfer from posterior temporal areas to inferior frontal areas in ~20-30 ms (Matsumoto et al., 2004). The drawback of ERPs is the low spatial resolution on the basis of dispersed topographical information due to the high resistance of the skull to transmit the electric currents. In order to analyse the underlying neural source activity, mathematical algorithms to estimate the spatial locations and resolve the inverse problem are used (Michel et al., 2004). Several such solutions are available (for review, see Grech et al., 2008), applicable to EEG data recorded with a sufficient number of channels.

Lexical access and memory-trace activation have been comprehensively studied using ERPs, as well as with their magnetic counterpart event-related fields (ERFs) measured with MEG, to elucidate the temporal progression of the spoken word recognition. Most studies that time-locked the event-related responses to the word disambiguation/recognition point employed mismatch negativity (MMN) designs, such as the oddball presentation of frequently presented standards with infrequent deviant stimuli that critically differ from the standard by just a single acoustic-phonetic feature (Näätänen, 2001). The MMN response was first shown to reflect language experience related discrimination of phonemes (Näätänen et al., 1997; Winkler et al., 1999) such that native phonemes elicited stronger MMN responses than acoustically matched non-native phonemes. The finding that with MMN the activation of language-specific long-term memory traces for phonemes could be distinguished set path for investigations with spoken words (Pulvermüller & Shtyrov, 2006). Accumulative evidence of MMN responses to ignored spoken words and pseudo-words consistently demonstrated stronger MMNs to known words compared to pseudo-words in adults and children (Korpilahti et al., 2001; Pulvermüller et al., 2001; Shtyrov & Pulvermüller, 2002; Sittiprapaporn et al., 2003; Endrass et al., 2004; Pettigrew et al., 2004; Pulvermüller et al., 2004; Boudelaa et al., 2010). The latency

of the MMN differentiating word and pseudo-word responses in adults was relatively early at ~100-200 ms after the point in time when the speech input allowed for the disambiguation of lexical status (see, however, Korpilahti et al. (2001) for the word enhancement at a later latency in children). The stronger word response was suggested to reflect lexical access (and ignition of the distributed neuronal assemblies) of long-term memory traces for words. The smaller response for pseudo-words was explained by the absence of such long-term traces. Neural sources for the word-specific responses were localised in left-lateralised posterior temporal and inferior frontal cortices.

The above-mentioned studies utilised the passive listening set-up in which subjects were ignoring the spoken stimuli while focussing their attention on visual material. The enhanced response to words in comparison to phonetically well-matched pseudo-words in non-attend conditions implies early automatic spoken word recognition (Pulvermüller et al., 2006; Shtyrov, 2010). Interestingly, for attended spoken stimuli, the difference in the early responses to words and pseudo-words was reversed – i.e. enhanced responses were elicited by pseudo-words compared to words (Garagnani et al., 2009; Shtyrov, et al., 2010a). Moreover, the early response to attended pseudo-words was greater than to ignored pseudo-words, whereas no such modulation by attention was observed for known words. This effect was also shown in the case of involuntary attention shifting to the spoken stimuli (Shtyrov et al., 2012). Taken together, the resilience to attentional effects on the early known word responses provides further support of automatic word recognition in the brain. Moreover, evidence from event-related responses indicates near-simultaneous access of the word-form and its meaning (e.g. Pulvermüller et al., 2005; Shtyrov et al., 2004, 2014), confirming the often used term ‘lexico-semantic processing’ to indeed be somewhat parallel in the perception of known words (Pulvermüller, 2001).

The required extensive repetition of stimuli for the purpose of obtaining a satisfactory signal-to-noise ratio of the ERPs, makes oddball paradigms time-consuming and prone to perceptual learning effects (Garrido et al., 2009). Furthermore, several studies have presented similar response patterns to lexical items with basic ERPs as was demonstrated with the MMN (e.g. Endrass et al., 2004; Garagnani et al., 2009; Shtyrov et al., 2012; Shtyrov, et al., 2010a). Importantly, MacGregor et al. (2012) showed the lexical effect with a large number of words and

pseudo-words by presenting each item only once. The averaging of responses separately for words and pseudo-words was enabled by careful control of acoustic-phonetic properties between the two types of stimuli. The earliest response indexing lexical access was detected only 50-80 ms after the auditory input was sufficient to identify the words. This result indicates extremely fast access of long-term lexical memory traces in the neocortex.

## **1.2.2 NEURAL IMPLICATIONS OF REPEATED EXPOSURE TO WORDS**

In order to explain how different lexical frequencies of words shape the neural network leading to the different behavioural recognition rates, the neural events underlying the effect need to be understood. The reactions of the brain to recurrent encounters with a word presumably change in the course of exposure, which may reflect the plastic changes in the synaptic level that are necessary for the formation of memory traces (Hebb, 1949; Pulvermüller, 1999). It is not clear if short exposure to new words is sufficient to change the neural responses. This initial phase of response dynamics is not well understood.

When a stimulus is repeated, the activity of the responding neurons is usually reduced (Grill-Spector et al., 2006). This is called repetition suppression, or repetition priming (Maccotta & Buckner, 2004). Indeed, Gagnepain et al. (2008, 2011) found a reduction of activation in the left STG for repetition-primed known words. While the bulk of behavioural repetition priming studies concentrated on repetition as a means of activating pre-existing representations (Schacter & Buckner, 1998), another line of research has evinced repetition priming as a learning mechanism for new information (Wiggs & Martin, 1998). Regarding novel word learning, even amnesic patients showed priming effects for novel words (Haist et al., 1991; Keane et al., 1995), suggesting that this implicit learning mechanism relies on neocortical structures. Crucially, however, neuroimaging studies showed that the neural activation to repetition of novel unfamiliar items *increased*, not suppressed (Henson et al., 2000; Henson, 2001; Gagnepain et al., 2008). In other words, repetition of new items (e.g. unfamiliar faces, unknown words) leads to an enhancement of neural activation. This probably indicates that pre-existing, item-specific, neural circuits are not present and

thus cannot be activated in the first place, while repeated exposure may, in turn, lead to the formation of such circuits, i.e. memory traces.

### **1.3 WORD LEARNING**

The development of lexical memory traces is a prerequisite for speech comprehension. Acquisition of new words is fast in childhood; learning to associate a novel word with meaning was shown to occur after just a few exposures (Carey & Barlett, 1978; Dollaghan, 1985), even in infants prior to speech onset (Woodward et al. 1992). Learning to associate novel words with specific referents is called ‘fast mapping’. Learning of new words continues throughout life as novel words, such as ‘blog’ or ‘tweet’, become frequently used in the language environment. The fast mapping ability is preserved in adulthood (e.g. Ramachandra et al., 2010). Such fast acquisition of novel words was also observed in ERP studies in which novel words were introduced within only a few exposures in sentence context that enabled the discovery of their meaning (Mestres-Missé et al., 2007; Borovsky et al., 2010). These studies indicated a neural correlate of learning as the N400 response to the novel words changed to resemble that elicited by known words. The N400 response is a temporally unspecified ERP deflection, peaking at ~400 ms after stimulus onset, assumed to reflect lexico-semantic access, selection, and integration (Lau et al., 2008).

The semantic content of new words does not, however, always become evident during learning. Indeed, semantics is not always required for word learning to occur: Non-associative language learning has been suggested by studies demonstrating novel word segmentation through probabilistic regularity extraction from attended streams of spoken syllables (Saffran et al., 1996; De Diego Balaguer et al., 2007; Cunillera et al., 2009; Lopez-Barroso et al., 2011). In these studies, multisyllabic combinations, which followed native language rules in their phonological and phonotactic make-up, were extracted within a few minutes of exposure. Learning was indexed by N400 dynamics: A rapidly established response increase was detected to learnt word-forms compared to a smaller response to random syllable combinations (Cunillera et al., 2009). Another study showed equivalent N400 responses to newly learnt and known words than to pseudo-words (De Diego Balaguer et al., 2007). The learning effect was also manifested by the successful recognition of the segmented word-forms (Saffran

et al., 1996; Lopez-Barroso et al., 2011). Moreover, automaticity of this kind of learning was proposed by a study where the speech stream was ignored during exposure, after which above chance recognition of the novel words was observed in children and adults (Saffran et al., 1997). While such learning of regularities and rules is inherent for language learning, acquisition of novel words through statistical regularity extraction cannot accommodate to learning situations where such operations are not required, e.g. when isolated word-forms are presented.

### **1.3.1 NEURAL MACHINERY OF WORD LEARNING**

The complementary learning systems account (CLS) of word learning in adults (Davis et al., 2009), arising from a more general CLS model (McClelland et al., 1995), proposes that the encoding of new words relies on subcortical medial temporal lobe structures (including the hippocampus) and is followed by a slow integration of the newly encoded words into the mental lexicon by the neocortex by virtue of an offline consolidation period. Sleep, as opposed to mere passage of time, is proposed to be fundamental for successful consolidation of the novel word memory traces to attain word-like representations (Dumay & Gaskell, 2007; Davis et al., 2009; Henderson et al., 2012). According to these studies, lexical integration has occurred when reaction times to the newly learnt novel words are slower in tasks requiring their activation than those to non-learnt novel items, which can be distinguished fast from the lexical competitors in the existing lexicon. However, with learning regimes (both fast mapping and non-associative ones) that prompted simultaneous activation of existing lexical competitors and the to-be-learnt novel words, integration of the newly learnt words was established within the same day without sleep-related consolidation (Lindsay & Gaskell, 2013, Coutanche & Thompson-Schill, 2014). This indicates that rapid development of neocortical memory circuits for novel words may be possible during exposure over a short period of time.

Results from hemodynamic studies have argued for the critical involvement of medial temporal lobe in the encoding phase of novel words (Breitenstein et al., 2005; Davis et al., 2009). More successful associative learning of novel words paired with objects correlated with sustained activation of the hippocampus (Breitenstein et al., 2005). However, a reduction in hippocampal activity was observed already between

the first and the following exposure to the novel word, the decline in activation continuing over several repetitions (Davis et al., 2009; see also Paulesu et al., 2009). This implies that hippocampus is relevant only in the very initial encoding of novel word-forms in learning conditions not involving episodic memory. This is supported by findings of intact repetition priming used in learning novel items (e.g. novel words; Haist et al., 1991) in amnesic patients with hippocampal damage (Squire, 1992). More recently, patients with damage in the hippocampal system with a related deep anterograde amnesia showed intact fast mapping (Sharon et al., 2011), implying that rapid acquisition of novel words associated with meaning can be accomplished by recruitment of the neocortical system, irrespective of hippocampal involvement.

### **1.3.2 LEARNING OF NON-NATIVE WORDS**

The learning of non-native languages is customary, and beneficial, in the global world of today. Non-native language (L2) learning entails words with unfamiliar phonology, and, especially in adults, is often more effortful than learning new native words. The adult brain is put to the test by the requirement to attach meaning to new word-forms but also by the need to learn new phonological-phonetic speech contrasts (i.e. phonemes) that distinguish words from each other. Studies have shown significant individual variability in learning to discriminate novel phonetic contrasts (Golestani & Zatorre, 2009). More successful learning was negatively correlated with hemodynamic activation in left inferior frontal areas and posterior MTG after learning, which was suggested to manifest increase in the processing efficiency of the newly acquired contrasts (Golestani & Zatorre, 2004). Better discrimination of L2 contrasts (learnt within natural language acquisition) in early bilinguals was associated with better discrimination of novel contrasts of a foreign language (Díaz et al., 2008).

When learning a non-native language, exposure to such phonetic contrasts in isolation, however, is not common. In contrast, they are embedded to word-forms that may constitute only novel phonemes but more probably familiar phonemes present in the native language as well. For this reason studying word learning with stimuli that comprise unfamiliar phonemes and phonology, is essential. So far, the neural learning effects of L2 comprising novel phonemes have mostly been investigated with written L2 words (e.g. McLaughlin et al., 2004; Bartolotti et al., 2016). Processing of such

novel written items, including possible contribution of incorrect phonemic conversions, however, may not be fully consistent with the processing of spoken L2 words. In studies of intensive L2 learning programs of both written and spoken language, greater increase in brain structures as a consequence of better foreign language acquisition was found in the right hippocampus and left STG (Mårtensson et al., 2012), and on the other hand, in right posterior IFG, as well as enhanced white matter connectivity of posterior STG, supramarginal gyrus, and caudate with this frontal region (Hosoda et al., 2013).

Research on factors that promote the establishment of the observed neural learning-related changes is, however, lacking. Some behavioural evidence suggests that individuals with non-native language experience outperform monolinguals in learning novel unfamiliar words of a yet new language, demonstrated with associative learning routines (Papagno & Vallar, 1995; Van Hell & Mahn, 1997; Kaushanskaya & Marian, 2009a, 2009b). Thus, the existing neural language architecture of the learner may affect how efficient learning novel non-native words is.

### **1.3.3 WORD LEARNING IN DYSLEXIA**

Developmental dyslexia is the most common learning disorder characterised by a specific difficulty in reading and writing while general intelligence is intact (Shaywitz & Shaywitz, 2016). It persists over development and is strongly heritable with a neurobiological basis (Habib, 2000; Gabrieli, 2009). The widely acknowledged core neurocognitive impairment in dyslexia is deficient phonological processing (Snowling, 1998; Vellutino et al., 2004; Ramus et al., 2013). Speech is considered unaffected in dyslexia, but longitudinal studies show delayed language acquisition and vocabulary development in children at-risk for dyslexia (Elbro et al., 1998; Gallagher et al., 2000). In a similar vein, an extensive number of behavioural studies have reported word learning deficits in dyslexic children and adults (Vellutino et al., 1975, 1995; Aguiar & Brady, 1991; Mayringer & Wimmer, 2000; Messbauer & de Jong, 2003; Elbro & Jensen, 2005; Di Betta & Romani, 2006; Ho et al., 2006; Li et al., 2009; Howland & Liederman, 2013; Litt & Nation, 2014). In these studies, dyslexics performed worse than normally reading peers in learning to associate novel words with referents. The slowness in learning was specific to visual-verbal and verbal-

verbal associations, with unimpaired performance in learning novel non-verbal associations (Messbauer & de Jong, 2003; Li et al., 2009; Litt & Nation, 2014). Most studies reported an impairment only in learning novel words and not in verbal learning of known words (see, however, Messbauer & de Jong (2003) for worse learning of known words as well). Moreover, long-term retention of the learnt novel words was unimpaired (Aguilar & Brady, 1991). Altogether, the research indicates deficient learning of novel phonological word-forms, not semantic associations, in dyslexia.

Despite of the vast evidence for a word learning impairment in dyslexia, the paired-associate learning tasks cannot unambiguously resolve at which stage of learning the deficit originates: at the initial encoding of the verbal input, maintenance of the encoded input for a short period of time, retrieval of the encoded input, generating the output of the retrieved material, or some combination of these. Thus far, there are no neuroimaging studies investigating the neural basis of the word learning deficit in dyslexia. By employing a carefully controlled ERP design, the processing stage(s) impeding the word learning can be elucidated.

#### **1.3.4 RAPID NEURAL DYNAMICS FOR EXPOSURE TO NOVEL WORDS**

While studies using semantic contexts to learn new lexical items showed that the acquisition of novel lexico-semantic forms can take place within only a few exposures (Mestres-Missé et al., 2007; Borovsky et al., 2010), it remained unknown whether semantic associations are necessary for the successful learning of novel word-forms or if rapid learning of mere phonological forms could occur. First evidence indicating rapid perceptual learning of novel word-forms without imposed or acquired meanings were shown with an indirect measure of learning, an ERP response enhancement to novel words through 160 repetitions (Shtyrov et al., 2010b). At the same time, the neural response to known words showed no significant change, with an inclination to decrease over the course of exposure. The rapid learning effect was underpinned by enhanced source activation in the left-lateralised perisylvian cortex. This cortical correlate of learning, counteracting the suppression usually occurring in response to repeated auditory stimulation (Haenschel et al., 2005; Garrido et al., 2009), was suggested to demonstrate rapid formation of a new neuronal circuit for the newly



introduced linguistic item. The effect was replicated with more tokens and showed specificity to linguistic material as exposure to an unfamiliar non-speech stimulus, modified from the speech signal in its acoustic properties, did not establish response changes (Shtyrov, 2011). In these two studies, subjects ignored the novel spoken word-forms and focussed their attention on visual stimulation, and, therefore, it can be suggested that the neural learning took place without conscious effort. The response exhibiting the increase occurred at ~70-140 ms after word divergence point (Shtyrov et al., 2010b; Shtyrov, 2011), matching the latencies of lexical access reported in earlier studies (see Section 1.2.1). Similar learning-related dynamics was acquired in a tonal language (Yue et al., 2014).

The results show marked resemblance with the automatic spoken word recognition results (reviewed in Section 1.2.1.), indicating early automatic memory-trace formation for novel lexical items. The studies did not, however, include any measures of behavioural memory performance in order to investigate the correspondence between the rapid neural dynamics and subsequent recollection of the novel words. The automaticity account also bids further examination on how focussed attention on the stimuli may affect the neural processing changes during exposure. Furthermore, several other cognitive factors may influence the individual neural patterns of response development, possibly revealing more detailed information on the plastic capacity and function of the neural circuits within the language network of the brain.

## 2 AIMS OF THE THESIS

The general aim of the current thesis was to investigate the effect of short- and long-term exposure to spoken words on brain responses that presumably reflect word memory-trace activation in the human neocortex. Cortical processing of known as well as novel words (pseudo-words) with different kinds of phonological as well as exposure-related properties was investigated in adults and children using high-resolution EEG in combination with behavioural and neuropsychological measures. Using acoustically and phonetically carefully matched spoken stimuli, the neural responses reflecting word recognition were obtained by time-locking the ERPs to the divergence points that distinguished the tokens from each other as well as from other items in the lexicon. Neural dynamics of the different stimulus types were studied in conditions with distinct demands of focussed attention on the stimuli, and in subjects with varying language experience and reading ability. The aim was to determine the connections between various putatively influential background factors and the neural dynamics elicited by the experimental word-forms.

More specifically, the aim of STUDY I was to determine the effect of word frequency, i.e. the occurrence of a word in a language, on the strength and temporal dynamics of memory-trace activation for spoken words. This was attained by contrasting ERPs to spoken words with higher vs. lower frequency, and their pseudo-word analogues. In the Hebbian learning framework, the more a word is used and encountered, the stronger the internal connections of the memory trace develop. This assumption leads to a direct hypothesis of stronger neural memory-trace activation for words with high frequency of occurrence and weaker activation for less frequent words. Hence, greater negative-going response amplitude, presumably reflecting stronger memory traces, was expected for words with higher frequency as opposed to those with lower frequency. Moreover, pseudo-words were expected to elicit weaker response than the words. Furthermore, contrasting the responses to the different lexical types, the speed of lexicality processing was assessed. This way, lexical access in the brain for known words differing in the extent of long-term exposure, and contrastively, brain activations for pseudo-words that lack such existing memory traces were examined.

STUDY II investigated rapid formation of memory traces for novel words through brief (~30 min) but extensive perceptual exposure. Responses to both novel and known word-forms at early and late stages of exposure were compared, and an increase in response negativity was assumed to reflect memory-trace formation, as indicated by previous research (Shtyrov et al., 2010b; Shtyrov, 2011; Yue et al., 2014). To test this assumption, memory performance on the word stimuli after exposure was measured with free recall and recognition tasks. Possible differences in how phonological make-up of spoken stimuli affects the neural dynamics was scrutinised by presenting novel word-forms with either native or non-native phonology. Notably, no semantic meaning was assigned or learnt for the novel words, with the aim to study purely phonological-lexical word-form processing. Moreover, the effect of attention was investigated by modifying its direction in two listening conditions, in which the subjects either ignored or attended on the spoken stimuli. Attention was hypothesised not to have a considerable effect on the rapid neural increase for novel words due to previously shown robust increase for ignored novel words. Further aimed at validating the proposal that the neural response increase really indicates word memory-trace formation, individual neural response changes to novel words were regressed on the measures of memory performance.

STUDY III probed possible effects that previous language experience may have on the exposure-induced neural dynamics for novel words. Factors delineating experience in learning non-native languages, i.e. the number of languages and their learning onsets and acquired proficiencies, were obtained and regressed against individual neural increase to novel non-native and native word-forms. Based on previous reports of second language learning shaping the language networks in the brain, it was hypothesised that experience in multiple languages besides mother tongue would show beneficial effects in learning novel words with unfamiliar phonology. Modelling the influence of the background factors separately for novel words with either familiar or unfamiliar phonology, the aim was to determine if previous foreign-language learning experience is associated with novel word-learning capacity in general or in a specific manner depending on the phonological familiarity of the word input.

In STUDY IV, neural responses to an auditorily repeated novel word-form with native phonology were investigated in children with or without dyslexia. Children

with typical reading and writing skills (controls) were expected to show rapid increase in the response to the novel word, similarly to adults, or even faster. On the basis of the phonological processing and word learning deficits reported in dyslexia, the short passive exposure (11 min) to the novel word-form was hypothesised to show an impaired lexical memory-trace formation dynamics compared to the controls.

## 3 METHODS

### 3.1 SUBJECTS

All participants were native Finnish speakers. STUDIES I-III consisted of healthy adults, and STUDY IV of two matched-groups of school-age children with or without dyslexia. None of the subjects had language-related, neurological, or psychiatric disorders (aside from dyslexia in the dyslexic children group). All reported normal hearing and normal/corrected-to-normal vision. The subjects in STUDIES I-III were right-handed, assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). In STUDY IV, all subjects reported right-handedness except for one left-handed in each group.

Inclusion criteria in STUDY IV required no neurological (including specific language impairment) and psychiatric disorders (excluding mild to moderate depression, and dyslexia in the dyslexic group) in first-degree relatives. All subjects in STUDY IV attended normal school and had non-verbal IQ of  $> 85$ . In the dyslexic group, 19 subjects had received special tuition in school, and one in the control group for mathematics. The dyslexic group consisted of 11 subjects previously tested for dyslexia by a psychologist or special education teacher; a licenced psychologist confirmed the rest to have dyslexia with the test battery of the study. Children showing signs of other language-related problems were excluded.

All STUDIES were approved by the Ethics Review Committee for Human Sciences of the University of Helsinki and were carried out according to the Declaration of Helsinki. Written informed consent was obtained from subjects in STUDIES I-III and from the guardians of subjects in STUDY IV, as well as an oral informed assent from the participating children. All subjects were remunerated for their participation. Table 1 summarizes subject information.

**Table 1.** Subjects in Studies I-IV.

<b>Study</b>	<b>N</b>	<b>Males</b>	<b>Mean age (SD), range in years</b>
<b>I</b>	18	10	32 (10.1), 19-53
<b>II</b>	22	10	24 (3.9), 19-32
<b>III</b>	22	10	24 (3.9), 19-32
<b>IV Control</b>	21	10	11 (1.0), 9.1-12.2
<b>Dyslexic</b>	21	11	11 (1.1), 9.6-12.8

All subjects had Finnish as their native language and came from monolingual families and had not been excessively exposed to non-native languages in early life, e.g., by attending school in non-native language or living in non-native environment. However, in accordance with the standard Finnish school system, all adult subjects had studied two or more non-native languages.

Subjects in STUDY III reported the non-native languages they had learnt, learning onset (age of acquisition, AoA) and self-evaluated proficiency (with a scale 1 = basic, 2 = passable, 3 = good, 4 = commendable, 5 = excellent) in each language. These results were used to investigate the relationship between the different language background measures and the neural response dynamics of novel word-forms.

### **3.2 STIMULI**

The spoken word stimuli in STUDY I were disyllabic known words and unknown pseudo-words with native phonology, with a CV\_CV (C = consonant, V = vowel) structure, where underscore ( \_ ) marks a geminate stop between the syllables (also known as ‘double consonant’, i.e. CC in orthographical form). In STUDIES II and III, the word stimuli were CVCV and, in addition to the native types, there were novel word-forms (pseudo-words) with unfamiliar non-native phonology, acoustically balanced with the other stimuli. The pseudo-word stimulus in STUDY IV was a tri-syllabic CVCVCV word-form. Word tokens are described in Table 2. In all studies, the consonants of the second syllable were plosives, enabling the use of cross-splicing of identical syllables across different stimuli (cf. use of fricatives, Steinberg et al., 2012). Cross-splicing was applied to fully control for the acoustic make-up of the stimuli such that identical first syllables could be combined with identical sets of second syllables and, as a result, the identity of the word-form could not be identified

before the second syllable. This also enabled time-locking of the neural responses accurately to the second syllable onsets, which thus served as disambiguation (or divergence) points – the times, when acoustic information starts to allow for word-form identification among other similar stimuli.

In STUDY I, identical sets of second syllables were used in the context of two different first syllables the combination of which defined the identity of the specific items. Thus, any differences between ERPs to two identical second syllables were due to lexicality, and not acoustic-phonetic differences. Also, this way the known words with different word frequencies had direct phonological pseudo-word analogues. In STUDY II, the native stimuli were created such that identical first and second syllables were cross-spliced in different order which created balanced sets of known and novel (pseudo) word-forms, the identity of which could only be distinguished at the second syllable onset. Likewise, the same second syllables were used for the novel non-native forms, but for these items the first syllables were different as they embedded non-native phonology critical for this word-type. Both types of these novel word-forms were used in STUDY III as well. Two sets of stimuli were created for the two experimental conditions in a counterbalanced fashion. In STUDY IV, neural responses to a single novel word-form were analysed. The constant structure of the word-form, constructed by cross-splicing a single syllable thrice consecutively, warranted that mere acoustic-phonetic differences between the syllables of the word-form could not elicit response differences for each embedded syllable.

**Table 2.** Word stimuli. Studies II and III had two stimulus sets of each word-type (known, native novel, non-native novel) for the two experimental conditions. The same novel tokens were used in Studies II and III. The | in the non-native items separates the syllables that were used for morphing the non-native sounding syllable. Note that the sound of the resulting morphed syllable cannot be directly deduced from the native syllables used in the morphing process.

Study	Known words	Native pseudo / novel word-forms	Non-native pseudo / novel word-forms
I	Lappu (scrap, tag) Lappi (Lapland) Lakko (strike) Lakki (cap) Lakka (lacquer, cloudberry) Lappo (siphon) Latte (café latte)	Leppu Leppi Lekko Lekki Lekka Leppo Lette	
II	Keto (meadow)      Kyky (ability) Peti (bed)            Käpy (pine cone) Poka (frame)        Piki (pitch) Pupu (bunny rabbit)    Täti (aunt) Teko (action)        Pöppö (bug)	Teto      Käky Keti      Kypy Puka      Täki Popu      Pöti Peko      Pipö	Pi ta-to      Te pa-ky Pö pu-ti      Pö pu-py Te pa-ka      Tö pu-ki Tö pu-pu      Pi ta-ti Pu pä-ko      Pu pä-pö
III			
IV		Tatata	

A female native Finnish speaker uttered the speech stimuli. In STUDIES I-III, the first syllables were uttered in isolation and the second syllables were produced with a preceding vowel that was different from the vowels in the actual experimental first syllables. This ensured that no bias was created by co-articulation from the vowel preceding the second syllable to the final stimuli but at the same time, the natural pitch contour for the second syllables was obtained. The final word-forms were produced by cross-splicing the first and second syllables in succession with a silent closure in between. In STUDY I, the first syllables were 230 ms, silent closure 270 ms, and second syllables 200 ms in duration (word-form duration 700 ms). Such extended silence between two syllables establishes a geminate stop that is typical in Finnish words and is semantically distinct from a word with the same phonemes but with a shorter silent gap. In STUDIES II and III, the first syllables were 145 ms, silent gap 75 ms (which does not create a geminate stop perception), and second syllables 145 ms (word-form duration 365 ms). The non-native syllables were constructed from native syllables by morphing 50 % of sound information from each original syllable using



Tandem-STRAIGHT algorithm (Kawahara et al., 2008), which created a CV structure with unidentifiable phonemes (i.e. not included in the native phonemic repertoire) that were at the same time balanced acoustically with the native set. Additionally, target stimuli were created for the active listening task in the attend condition used in STUDIES II and III. The target sounds were constructed from the word-forms by prolonging the silent closure between syllables, which corresponds to the acoustics of geminate stop before a consonant, and thus was possible for the subjects to detect.

In STUDY IV, the middle syllable of a naturally uttered *tatata* was used for stimulus preparation. The duration of the syllable was 100 ms, and the final word was produced by cross-splicing the same syllable three times consecutively with 50 ms silent gaps in between each syllable, resulting in word-form duration of 400 ms. Infrequent filler tokens were constructed by replacing the middle or final syllable with a modified one having a prolonged vowel duration, vowel identity, or pitch.

### 3.2.1 WORD FREQUENCY

The frequency of occurrence for the words in STUDY I was determined using two sources. First, word frequencies were acquired with the Lemmie query tool from the Language Bank of Finland corpus on newspapers published 1990-2000 (CSC – Scientific Computing Ltd, Espoo, Finland). According to the corpus, *Lappi* (153.86 instances per million (ipm), log-transformed 2.19) was the most frequent one, followed by *lakko* (119.46 ipm, log 2.08), *lappu* (10.44 ipm, log 1.02), *lakka* (7.58 ipm, log 0.88), *lakki* 6.15 ipm, log 0.79), *lappo* (0.07 ipm, log -1.15), and *latte* (0.04 ipm, log -1.40) as the most infrequent one. Additionally, a survey where native speakers ( $n = 73$ ) rated each word's productive as well as perceptive frequency on a scale 1-5 (1 = daily, 2 = weekly/monthly, 3 = sometimes, 4 = seldom, 5 = never) was implemented. The results of the questionnaire indicated the same three words as the most frequent as those according to the corpus: *lappu* with a mean frequency rating (F) of 2.52 (SEM = 0.06), *Lappi* (F = 2.73 (0.05)), and *lakko* (F = 2.76 (0.05)). Correspondingly, the more infrequent ones were *lakki* (F = 2.9 (0.08)), *lakka* (F = 3.04 (0.07)), *latte* (F = 3.12 (0.08)), and *lappo* (F = 4.38 (0.05)). Most raters found each of the pseudo-words as not part of the Finnish language (90-100% of all ratings) and their

frequency ratings were between 4.95 and 5.0 indicating that the pseudo-words were never used or encountered.

The novel word-form *tatata* used in STUDY IV disambiguates from words in the Finnish lexicon from the beginning of the second syllable. According to the Corpus of Finnish Magazines and Newspapers from the 1990s and 2000s (<https://korp.csc.fi/download/lehdet90-00>) there are only 19 words starting with ‘tat’ with a sum frequency of 0.6 ipm (log -0.22).

### **3.2.2 WORD DIVERGENCE POINTS**

In the study of spoken word processing, it is necessary to assess the time-point at which a word can be distinguished from other candidates starting with the same phonemes. This knowledge on specific words can be acquired with a ‘gating task’, in which increasing fragments of the word are presented, and after each successive pass the listener writes down what they heard and how confident they are of the judgement (Grosjean, 1980). ‘Isolation point’ is the fragment followed by correct response for the first time without subsequently changing their mind (Grosjean, 1980) and ‘recognition point’ the fragment for which the confidence of the response is  $\geq 80$  percent (Tyler & Wessels, 1983). In STUDIES I and II-III, we ran such gating tasks with 10 ms and 5 ms fragment increases, respectively, on independent subjects, who did not participate in the EEG studies ( $n = 5$  and  $3$ , respectively). According to the results, in STUDY I, the recognition point ranged from 30-40 ms after the second syllable onset. In STUDY II, the mean isolation point was 28 ms ( $SD = 1.72$ , range 10-50 ms) and mean recognition point 41 ms ( $SD = 2.29$ , range 25-50 ms) post second syllable onset. These data confirmed the isolation point to closely coincide with the plosive consonant in the beginning of the second syllable. Thus, we used the second syllable onset as the divergence point (DP), and henceforth the point to which the ERPs are time-locked to, as it was kept constant for all stimuli within each study. In STUDY IV, the lexical status can be defined from the second syllable plosive (see Section 3.2.2 for details), so the DP of the novel item was set at the second syllable onset. As the DP in STUDY IV could be defined a priori, no additional gating task was performed on either of the two children’s groups to minimise the experimental load.

### 3.3 NEUROPSYCHOLOGICAL MEASURES

Unlike the adult normally-reading subjects in STUDIES I-III, children in STUDY IV were tested with a comprehensive neuropsychological test battery for their cognitive and literacy skills. Their reasoning skills were measured with the WISC-IV (Wechsler, 2010) Perceptual Reasoning Index (PRI; subtests Block Design, Matrix Reasoning, and Picture Concepts) and Similarities subtest of the Verbal Comprehension Index. Phonological awareness was measured with the Phonological Processing task of NEPSY-II (Korkman et al., 2008). Rapid naming and switching were examined with the Rapid Automatized Naming and Switching tests (RAN subtests Colours, Letters, Numbers, and Object, and RAS subtests Letters-Numbers and Colours-Letters-Numbers; Ahonen et al., 2003). Verbal short-term and working memory was assessed with the WISC-IV Working Memory Index (WMI; subtests Digit Span and Letter-Number Sequencing) and NEPSY-II Word List Interference. Verbal learning and long-term memory were tested with Memory for Names subtest of NEPSY-II. Reading ability was assessed with Reading Fluency (Lukilasse; Häyrynen et al., 1999) that consists of reading a list of words as accurately and quickly as possible. Writing accuracy was assessed with Writing from Dictation (Lukilasse; Häyrynen et al., 1999), in which subjects write words and sentences dictated by the experimenter without time or repetition constraints. The subjects were tested on a separate day before the EEG experiment.

### 3.4 EXPERIMENTAL PROCEDURES

In STUDY I, a passive listening paradigm was employed in which subjects were instructed to ignore the sounds and concentrate on a silent film. Known and pseudo-word stimuli were divided in separate streams, which were further split in three blocks of equal length, and presented in alternating, counterbalanced order. In each block, every other stimulus was a frequent filler (*latte* or *lette* depending on the block, with a probability of 1/2), and every other one of the remaining tokens of the set, each having a probability of 1/6 within a block, presented in randomised order. Stimulus onset asynchrony (SOA) was 900 ms.

STUDY II had two experimental conditions differing in attention allocation to the speech stimuli. First, an ignore condition similar to that in STUDY I was conducted,

which was followed by an attend condition where subjects were instructed to carefully pay attention to the sounds and ignore the silent film on the background. In order to keep focus on the speech stimuli, subjects' task was to press a button whenever they heard a target stimulus that occurred with 7 % probability. At the same time, they were asked to memorise the word stimuli. The stimuli were presented in pseudo-randomised sequences of fifteen tokens in each stimulus set to ensure balanced occurrence throughout the session. Within a condition, each stimulus occurred 150 times; thus the exposure time in the ignore condition was ~32 minutes and in attend ~34 minutes. Presentation of the stimulus sets was counterbalanced between conditions across subjects. The mean SOA was 850 ms with a jitter ranging from 800 to 900 ms in 10 ms steps. After the ignore condition, subjects were unexpectedly asked to freely recall what they had heard after which a recognition memory task with 30 alternatives followed (including only native word types because the orthographical forms of the novel non-native items were not learnt). An identical procedure followed the attend condition, now however prompted in advance. In order to further assess subjects' direction of attention, they filled in a questionnaire about the contents of the film in both conditions. STUDY III exploited the same novel word-forms and procedure used in STUDY II.

Subjects in STUDY IV were exposed to the speech stimuli in an ignore condition, as in STUDY I. In the exposure session of 11 minutes, the novel word-form was repeated 540 times, amongst which infrequent fillers were presented with a probability of 30%. The stimuli were presented with an 800 ms SOA, jittered between 750-850 ms in 10 ms steps. In all STUDIES, stimuli were presented via headphones in an electrically and acoustically shielded room.

### **3.5 DATA ACQUISITION AND ANALYSIS**

Neural responses were recorded with a 64-channel active electrode EEG setup (Biosemi B.V., Amsterdam, Netherlands). Additional electrodes were placed on the mastoids and the tip of the nose. Vertical and horizontal eye movements were recorded with two electro-oculograms (EOG) placed below the right eye and next to the lateral canthus. The EEG was recorded with electrodes placed according to the international 10-20 system with an online reference at PO1, recording bandwidth of DC-104 Hz

and 512 Hz sampling rate. Data were down-sampled offline to 256 Hz. Noisy channels were interpolated, epochs with artifacts were discarded, and in STUDIES II-IV, principal component analysis (PCA; Ille et al., 2002) was used to correct for eye blinks. Next, data were pre-processed as shown in Table 3.

**Table 3.** Details of EEG data pre-processing and source modelling methods.

	<b>Study I</b>	<b>Studies II and III</b>	<b>Study IV</b>
Filter (Hz)	1–20	0.5–45	1–30
Eye blink correction	-	PCA	PCA
Re-reference	average of all channels	average of mastoids	average of mastoids
Epoch (ms)*	-50–450	-220–580	-50–750
Baseline (ms)*	-50–0	-220–0	-50–0
Artifact rejection threshold ( $\mu\text{V}$ )	$\pm 75$	$\pm 100$	$\pm 100$
Source modelling	L2 MNE	LORETA (Study II)	wMNE

\*All epochs and baselines denote latencies relative to the word divergence point. PCA = principal component analysis. (w)MNE = (weighted) minimum norm estimate. LORETA = Laplacian weighted minimum-norm algorithm.

In STUDY I, responses to the filler items that gave a background for the experimental stimuli were excluded from further analysis. Epochs for words with higher and lower frequency (three words in each case) were separately averaged together, and their pseudo-word counterparts similarly. Thereafter the signal of the low frequency words was subtracted from that of the higher frequency words, and the same was carried out for the pseudo-word counterparts in order to see if differences between the high and low frequency words were merely due to acoustic effects. Cortical sources of significant ERP effects were modelled with the L2 minimum-norm current estimate method (L2 MNE; Hämäläinen & Ilmoniemi, 1994). The MNE solutions were calculated using a three-layer boundary element model (BEM) with triangularised grey matter surface of a standard brain (Montreal Neurological Institute, MNI), and restricted to grey matter surface.

In STUDY II, the first and last quarter of data from each condition were subjected to further analyses. Epochs of each word type (known, novel native, and novel non-native) were averaged together separately per quarter. Cortical source activity underpinning the ERP effects was modelled with Laplacian weighted minimum-norm

algorithm (LORETA; Pascual-Marqui et al., 1994) using a standard four-shell ellipsoidal head model.

In STUDY IV, the continuous data were also divided into four blocks of the same length. Responses to fillers were discarded from further analyses. The epochs of the novel word-form responses were averaged together per block for each group of subjects separately. The underlying cortical source activity of the found sensor-level effects was estimated with weighted minimum-norm current estimate (wMNE; Lin et al., 2006). A three-layer BEM with a grey matter surface of an age-appropriate (10.5 years) MRI template (Neurodevelopmental MRI Database; Richards et al., 2016) was utilised to calculate the source solutions.

### **3.6 STATISTICAL ANALYSES**

In all STUDIES, mean amplitudes of sensor- and source-level responses were extracted from a 20 ms time-window around the specified latencies. Details of each STUDY are below.

In STUDY I, the peak latency was defined at the electrodes showing the most prominent response for the averaged difference (higher vs. lower frequency) signal. The mean amplitude values were submitted to analysis of variance (ANOVA) with Lexicality (word vs. pseudo-word) and Frequency (higher vs. lower) as within-subjects factors. This indicated the response latencies at which significant differences between the two frequency categories occurred. Additionally, Pearson quotients of correlations between the questionnaire ratings and the corresponding word response amplitudes were analysed with a group-level t-test. In order to assess the effects of other relevant psycholinguistic factors besides frequency, similar procedures were administered on additional measures: number of phonological competitors and cohort size (obtained from the Lemmie corpus), as well as abstractness, concreteness, valence, arousal, sensation, and action-relatedness based on assessments acquired from native speaker ratings ( $n = 24$ ).

Further, lexicality effects were investigated by comparing the average ERPs for all words vs. pseudo-words. Similarly to the analysis of frequency effects, the latency for the mean amplitude calculation was acquired from the peak of the subtracted average

signal, and the mean amplitudes were submitted to the same ANOVA (Lexicality  $\times$  Frequency).

In STUDY II, response peaks were determined based on averaged responses per condition, stimulus type, and exposure time, using channels with the most pronounced responses. Individual mean response amplitudes for each deflection were calculated from this average signal and used in further analysis. Response magnitudes were compared using repeated-measures ANOVA (rmANOVA) with factors Lexicality (known vs. novel native vs. novel non-native)  $\times$  Attention (ignore vs. attend)  $\times$  Exposure time (early vs. late in exposure) in order to determine whether a significant response increase during the exposure session was established for the novel word types. Topographical distribution differences were analysed with similar rmANOVAs that employed additional factors Hemisphere (left vs. right) and Anterior-posterior (4 most anterior vs. 4 most posterior channels in the hemispheric ROIs), displayed in Fig. 1. Source activations harnessing exposure-related changes were analysed with a priori chosen cortical locations in inferior frontal and posterior temporal areas, which are critical in spoken word recognition according to previous research (Pulvermüller et al., 2003; Hickok & Poeppel, 2007; Price, 2010; MacGregor et al., 2012). Mean source current densities in these locations were calculated from 7 mm radius voxels around source peaks at each source estimate and time-window. The acquired current densities were submitted to Lexicality  $\times$  Attention  $\times$  Exposure time  $\times$  Source location (temporal vs. frontal)  $\times$  Hemisphere (left vs. right) rmANOVA. Multivariate ANOVA, which does not assume sphericity, was used whenever this assumption was violated.

Learning accuracy and errors in retrieval of the words were examined after each condition using the measures of hit rate (HR) in free recall, and HR and false alarm rate (FA) in the recognition task (note that FA in free recall could not be defined due to indeterminate number of possible false responses). Furthermore, a measure of sensitivity reflecting the ability to discriminate correct recognitions from incorrect ones,  $d'$  ( $d' = Z(\text{HR}) - Z(\text{FA})$ ), was calculated. These indicators were analysed with separate rmANOVAs for each memory task with factors Lexicality of responses (known vs. novel native)  $\times$  Attention (ignore vs. attend)  $\times$  Validity of response (correct vs. incorrect in free recall; HR vs. FA in recognition task). Hit rates between memory tasks were analysed using factors Task (free recall vs. recognition)  $\times$  Lexicality  $\times$

Attention. Subjects' attention on the instructed modality in STUDY II was assessed from their answers to the questionnaire on the film content with paired t-test.

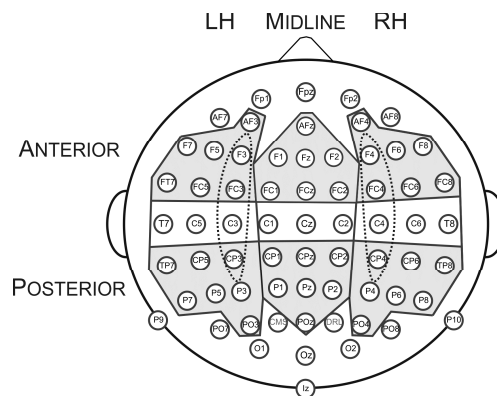
Finally, association between exposure-related neural response changes and memory performance was investigated by first calculating Pearson correlations between significant neural changes and behavioural memory indices. Measures that showed significant two-tailed correlations and filled assumptions for multiple linear regression were further analysed with stepwise linear regression analysis with the influence of age entered in the first step and in the next step, both age and neural response change.

In STUDY III, the same procedure of mean amplitude extraction as described in STUDY II were here applied only for novel stimulus types and the latencies showing learning effects. Due to moderate number of subjects, they could not be categorised into separate groups based on proficiency levels per language, AoAs, etc. Instead, average scores of each measure of the language history questionnaire were used in further analyses in order to take all learnt non-native languages into account. The possible effect of age on the language measures as well as on response changes was first tested with Pearson correlation. Similarly, the association between language variables and their relation to neural response changes was tested. In order to determine which language measures predicted neural response change significantly, variables with significant correlations were then entered into multiple linear regression analysis for each response change separately (two novel word-form types and two attention conditions). Differences in the structures of the resulting regression models between stimulus types and conditions were tested with Meng's *Z* for correlated correlation coefficients (Meng et al., 1992). Differences in the regression coefficients of specific predictors between models were analysed with Cohen's approach (Cohen, 1983).

In STUDY IV, individual peak latencies were determined as the most negative peak within an 80 ms time-window around the group average negative peak. This was implemented for each peak and block from a channel showing generally strongest responses. Latency differences were compared with rmANOVA Group (dyslexic vs. control)  $\times$  Block (1 to 4). Mean amplitudes from three large ROIs covering the distribution at midline, left, and right hemispheres with 17 channels in each, as depicted in Fig. 1, were used in the analysis. Neural dynamics between the beginning



and the end of exposure for each response and group was investigated by comparing the first and second half of exposure and further the first and second sub-block in each half. This was attained with an rmANOVA with factors Group  $\times$  Block (first vs. second half of exposure)  $\times$  Sub-block (first vs. second in each half)  $\times$  ROI (left, midline, right). Topographical distribution differences in the anterior-posterior plane were analysed from the ROIs showing the most prominent effects with a follow-up rmANOVA Group  $\times$  Block  $\times$  Sub-block  $\times$  Anterior-posterior (ROI of 7 most anterior vs. 7 most posterior channels). Greenhouse-Geisser correction was used when appropriate.



**Figure 1.** The channel ROIs with dotted outlines were used for hemispheric comparisons in Study II. The ROIs with solid outlines in the left hemisphere (LH), midline, and right hemisphere (RH), 17 channels in each, were used in Study IV. Further anterior and posterior ROIs are separated horizontally; channels at the C-line was excluded from the anterior and posterior ROIs. The layout of all channels render the arrangement used in all Studies.

Analysis of the neural activation increase corresponding to the effects in sensor-space employed difference source waveforms of individual global field power between the blocks with significant ERP enhancement. Mean current densities were extracted around individual peak latencies in each block. Planned comparisons of the mean current densities between the blocks were applied using one-tailed t-test for each BEM vertex. The resulting t-values at the centre of each source showing significant difference were corrected for multiple comparisons. The same analysis procedure for sensor- and source-space data was applied to subsequent negative responses, however using a 100 ms time-window for the initial peak latency search due to wider group average peaks.

Performance of the groups in the neuropsychological tests were compared with multivariate ANOVA (MANOVA) using normative standardised scores of WISC-IV and NEPSY-II, and multivariate analysis of covariance (MANCOVA) using raw scores with age as covariate for Reading fluency, Writing accuracy, RAN, and RAS (due to small sample sizes in normative standardisations). Associations between scores drawn from the reading and writing tests and significant sensor-level response changes separately for each group and across groups were investigated with separate linear regressions. First, age was controlled for by regression from the reading and writing scores and the residual scores were used as the predictor variables. Differences in significant regression coefficients between groups were analysed with univariate ANOVA.

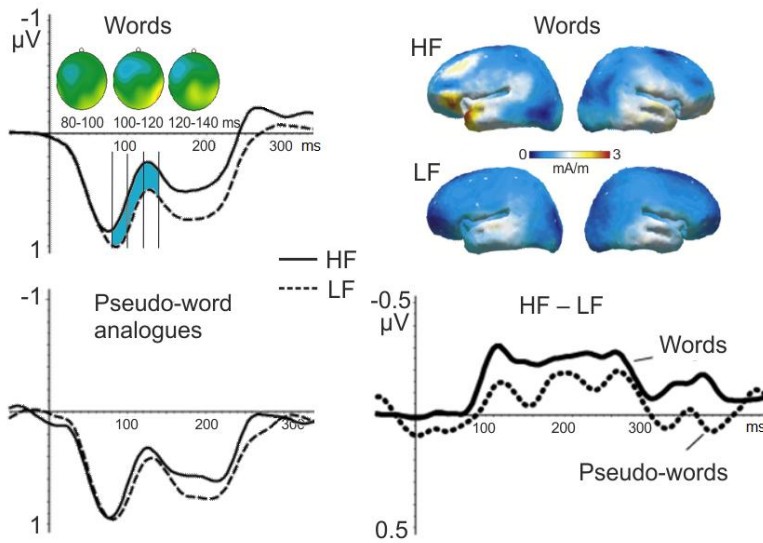
In STUDY I, ANOVAs were followed by separate planned comparisons, and in STUDIES II-IV post hoc pairwise comparisons. In all studies, sphericity assumption was assessed with Mauchly's test. Analyses of sensor-level effects were Bonferroni-corrected for multiple comparisons. Source-level analyses utilised Bonferroni in STUDY II and false discovery rate (FDR; Benjamini & Hochberg, 1995) in STUDY IV for multiple comparisons correction.

## 4 RESULTS AND DISCUSSION

### 4.1 STUDY I: THE EFFECT OF WORD FREQUENCY ON SPOKEN WORD MEMORY-TRACE ACTIVATION

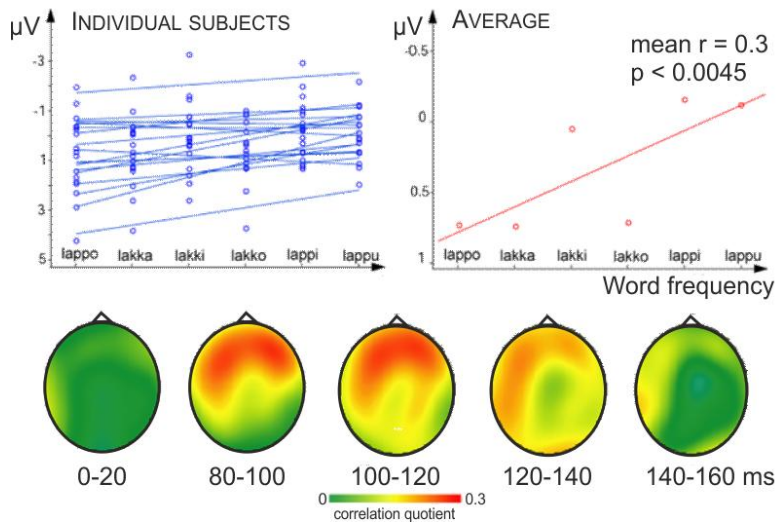
#### 4.1.1 FREQUENCY EFFECT

The difference curve of higher (HF) minus lower frequency (LF) words showed a maximal discrepancy between the items around 90-150 ms, peaking ~120 ms, at left frontal channels (Fig. 2). There was a significant Lexicality by Frequency interaction for this response ( $F(1,17) = 8.58, p < 0.01$ ) whereby the response to HF tokens was significantly more negative than to the LF ones but only in the case of real words. This dynamics was further investigated with planned comparisons by which the HF words had a more negative response than their pseudo-word analogues ( $F(1,17) = 5.73, p < 0.029$ ) whereas there was no difference between the LF items and pseudo-words ( $F(1,17) = 0.15, p > 0.7$ ). A significant main effect of frequency was established for words ( $F(1,17) = 5.47, p < 0.032$ ) but not for the pseudo-word analogues ( $F(1,17) = 0.56, p > 0.46$ ). Source analysis suggested that the frequency effect for known words was driven by left-dominant inferior frontal and anterior temporal and some more dorsal prefrontal cortical activations (Fig. 2).



**Figure 2.** Average responses from a representative channel FC3 for higher frequency (HF) and lower frequency (LF) words and their scalp topography difference, which peaks shortly after 100 ms (top left). Source reconstruction of the word frequency effects at 120 ms shows particularly left hemispheric activation in the inferior frontal, anterior temporal as well as in the precentral cortex to a lesser extent (top right). Average responses for the pseudo-word counterparts (bottom left) and difference curves of HF minus LF for both word types (bottom right).

A t-test of individual correlation quotients of individual response amplitudes at ~120 ms for the words and their frequency ratings showed a significant correlation ( $p < 0.0045$ , mean  $r = 0.3$ , Fig. 3). Running the same analysis with the pseudo-word counterparts did not produce any significance ( $p > 0.447$ ). Similar analyses with the other psycholinguistic variables did not produce any significant results either.



**Figure 3.** Correlations between word frequencies and individual subject response amplitudes and the average response amplitude (top). Scalp topography of the correlation quotients showing the left frontal frequency effect peaking shortly after 100 (bottom).

These results suggest that word frequency has a rather early effect on spoken word perception, shown by ERP dynamics detected  $\sim 100\text{-}130$  ms after the critical syllable onset. High frequency words elicited stronger neural responses at this latency than low frequency or pseudo-words, which presumably reflects stronger activation of the neural memory circuits for HF words in the neocortex (Hauk et al., 2006; Shtyrov et al., 2008). Considering the careful matching of the acoustic properties of the stimuli (duration, intensity, and fundamental frequency), and further the physically identical syllables completing the pseudo-words, the differences found between high vs. low frequency words were unlikely to result from differences purely in sensory information. Further, while the first syllables were not identical between the two stimulus types, they were exactly the same within the stimulus group, which largely excludes the possibility that the effect was driven by the first syllable. Importantly, this effect seems to be automatic in that it is demonstrated in a listening condition where the spoken items were ignored. This is supported by previous passive listening experiments with spoken known and pseudo-words suggesting automatic lexical access at  $100\text{-}150$  ms after stimulus identification (e.g. Pulvermüller et al., 2001; Shtyrov & Pulvermüller, 2002). The current result was later corroborated by Alexandrov et al. (2011) who showed similar frequency effect with unattended spoken

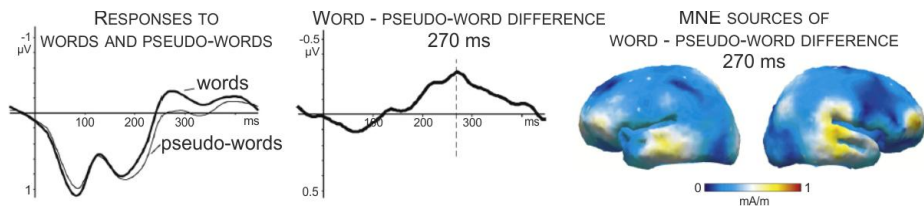
Russian HF and LF words. With acoustic-phonetically closely comparable spoken items, ERP-enhancement to a high-frequency word was elicited at < 150 ms latency. The current results also comply with findings of frequency effects at 110-190 ms in the visual domain (Serenó et al., 1998, 2003; Assadollahi et al., 2001, 2003; Hauk et al., 2004; Hauk et al., 2006; Penolazzi et al., 2007). It thus seems that frequency effects occur at similar latencies after DP in the auditory modality as after the presentation onset of visual words in the recognition process, supporting the account of word frequency effect being similar irrespective of modality (Connine et al., 1990).

The cortical sources giving rise to the word frequency effect were found predominantly in the left inferior frontal as well as bilateral anterior temporal cortices, accompanied by some prefrontal activation in the left hemisphere (Fig. 2). Indeed, previous studies using fMRI and EEG have found frontal (Kuo et al., 2003; Carreiras et al., 2006; Hauk et al., 2006; Hauk et al., 2008) and anterior temporal (Carreiras et al., 2006) areas to be associated with word frequency in the visual modality. Moreover, the functioning of the anterior temporal lobe has been found to be focal in the storage and access of lexico-semantic memory traces for words (Halgren et al., 2006; Lambon Ralph & Patterson, 2008). Whereas the frontal-anterior temporal pattern of activation was enhanced for HF words, the LF words showed no frontal and only weak temporal activation (Fig. 2). This implies frontal engagement during repeated exposure to (i.e. higher occurrence of) words that, at the same time, possibly strengthens the connections between temporal and frontal areas, leading to the distinction between high and low frequency word processing found here.

#### **4.1.2 LEXICALITY EFFECT**

Frequency-independent lexical effect was shown by the comparison of all known words and pseudo-words at the fronto-central channels. The enhanced negativity for known words over pseudo-words was found at 110-130 ms for the more frequent words, and, later, at ~270 ms, a negative response was found for the majority of the stimuli (Fig. 4). This effect was significant for all stimuli ( $F(1,17) = 5.07, p < 0.038$ ) but the very infrequent word *lappo*, which was rated almost as infrequent (4.38) as the pseudo-words (> 4.95 in a scale indicating use of the word with 5 = 'never'). The cortical sources underlying the lexical enhancement were localised in bilateral middle

temporal and inferior frontal regions. This later response showed no significant correlations with word frequency ratings.



**Figure 4.** ERPs to all words and pseudo-words (left) and their difference (middle). Source reconstruction of the difference peak at 270 ms (right).

Greater responses for ignored known words over pseudo-words had previously been found at such early latencies (~100-150 ms) in studies using high-frequent words (e.g. Korpilahti et al., 2001; Pettigrew et al., 2004; Shtyrov et al., 2005). Explanation for the lexicality effect found only for the HF words at the earlier latency could be that their lexical access is faster than that of LF words, generating this difference. Indeed, spoken LF words showed a delay in their maximal ERP response compared to HF tokens also in the study by (Alexandrov et al., 2011). The later lexicality effect is supported by studies in the visual domain showing LF vs. HF differences at 250-400 ms (Carreiras et al., 2005; Martín-Loeches et al., 2005; Wang & Yuan, 2008). This effect, covering both HF and LF words over pseudo-words, could reflect re-assessment of language information (Friederici, 2002; Barber & Kutas, 2007). Previous research shows considerable evidence on the involvement of STG and MTG in lexico-semantic word processing with coinciding frontal activations (Perani et al., 1999; Marinkovic et al., 2003; Pulvermüller et al., 2003; Scott & Johnsrude, 2003; Shtyrov & Pulvermüller, 2007; Price, 2010). The cortical sources for this effect originating from bilateral inferior frontal and temporal cortices indicate distributed memory traces for words across both cerebral hemispheres (Pulvermüller et al., 2004; Kellenbach et al., 2005).

## 4.2 STUDY II: RAPID FORMATION OF MEMORY TRACES FOR NOVEL WORDS IN DIFFERENT LISTENING CONDITIONS

### 4.2.1 NEURAL RESPONSES FOR KNOWN AND NOVEL WORD-FORMS

Two distinct responses were elicited by all word types at ~50 ms and ~150 ms in midline fronto-central channels, whereby amplitudes from a fronto-central sensor ROI (Fz, FCz) were used. At the early stage of exposure, the response at 50 ms to known words was stronger than that to the novel word-forms ( $p$ -values  $< 0.05$ ) and the magnitude of the response to the novel native word-forms was greater than that to the novel non-native ones ( $p = 0.028$ ). The effect of known  $>$  novel word-forms had, however, disappeared by the late stage of exposure, and responses to novel native word-forms were then strongest ( $p$ -values  $< 0.03$ ). A significant interaction of Lexicality by Exposure time ( $F(2,42) = 5.42, p = 0.008$ ) further confirmed the different dynamics in response magnitudes (Fig. 5). Namely, this interaction stemmed from a significant response increase to novel native word-forms between early and late stages of exposure ( $p = 0.0255$ ) and conversely, a decrease in the responses to known words ( $p = 0.022$ ). The responses to novel non-native word-forms did not manifest significant changes ( $p > 0.48$ ). Attention showed no interaction with lexicality and exposure time ( $F < 1.22, p > 0.3$ ) indicating that the response changes were similar across ignore and attend conditions.

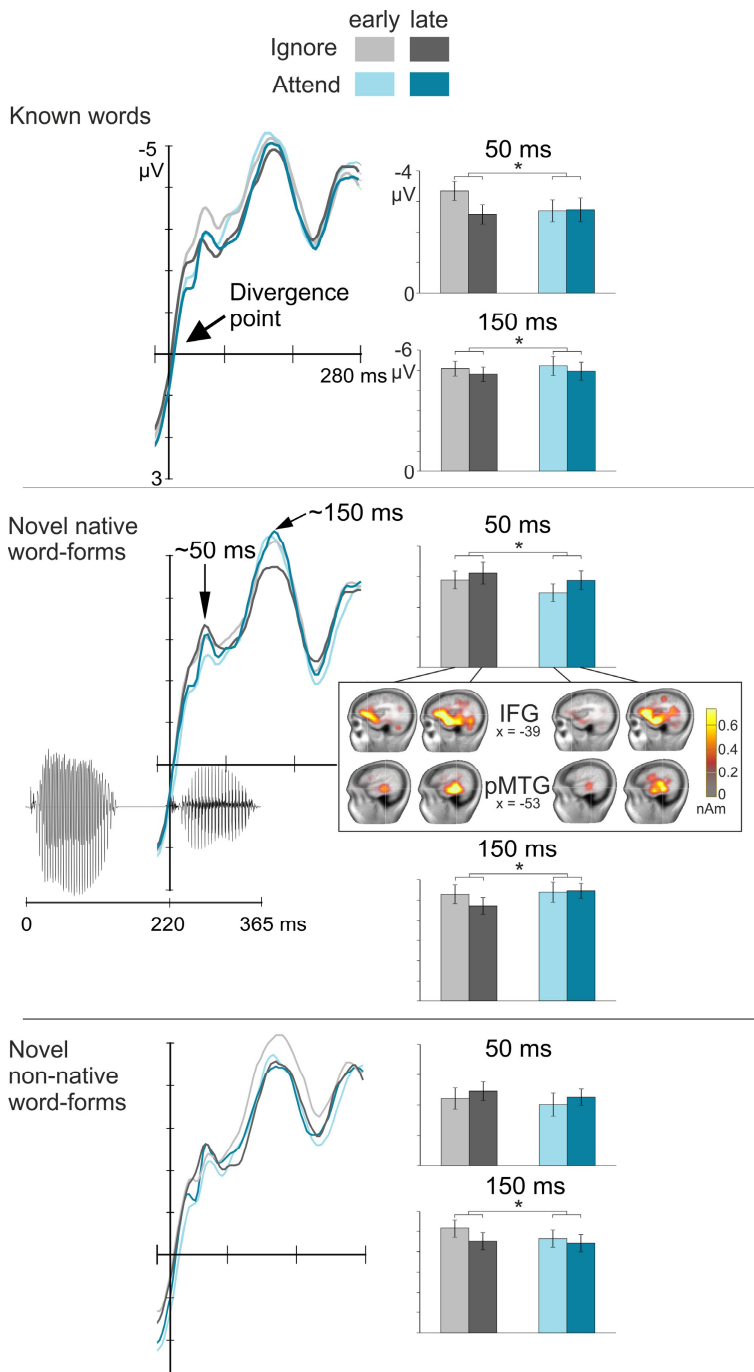
The second response phase at 150 ms, on the other hand, showed a significant interaction with Attention by Lexicality ( $F(2, 42) = 4.78, p = 0.014$ ). This response was smaller to novel non-native items than to native types in attend condition ( $p$ -values  $< 0.05$ ) but the responses to ignored stimuli showed no significant differences ( $p$ -values  $> 0.81$ ). Additionally, there was a trend for a greater response magnitude for novel native vs. known native word-forms in the attend condition, which did not reach full significance ( $p = 0.057$ ). Furthermore, the exposure induced a significant decline in responses across word types and conditions ( $F(1,21) = 5.81, p = 0.025$ ).

To ensure that the exposure-induced changes were not driven by dynamic changes to the first syllables (though not very likely due to the acoustically and physically well-matched stimuli and design), we ran the same analysis as above to responses time-locked to the first syllable onset. No interactions or main effects for exposure time



were found for either the first or second responses, confirming that learning-related dynamics were established only after the second syllable onset.

Reconstruction of the cortical sources underlying the significant sensor-level response increase to novel native word-forms at 50 ms showed a significant four-way interaction of Lexicality  $\times$  Exposure time  $\times$  Source location  $\times$  Hemisphere ( $F(2,20) = 3.58$ ,  $p = 0.047$ ) which localised significant enhancement in source current densities to novel native items in inferior frontal (IFG, BA45; Talairach coordinates  $x = -38.5$ ,  $y = 24.8$ ,  $z = 2.8$ ) and posterior middle temporal (pMTG, BA21;  $x = 52.5$ ,  $y = -31$ ,  $z = -11.3$ ) regions of the left hemisphere ( $p$ -values  $< 0.05$ ; Fig. 5). For novel non-native word-forms, a significant decline in source activation was found in the right IFG ( $p = 0.026$ ). Additionally, at early stages of exposure, activation to native word types was stronger in the left IFG than in the left pMTG, while this pattern had shifted to the right hemisphere by the end of the exposure, and for non-native items, this activation dominance was conversely shifted from right to left hemisphere between early and late exposure ( $p$ -values  $< 0.05$ ). Overall, the activation in the frontal source was greater than in the temporal one ( $F(1,21) = 11.25$ ,  $p = 0.003$ ). The response attenuation for known words at 50 ms or for all word types at 150 ms was not found to be underpinned by activation changes in the IFG and pMTG.



**Figure 5.** Response curves at early and late stages (average of first and last quarter ERPs, respectively) in ignore (grey shades) and attend (blue shades) conditions for each word type. Histograms show the response dynamics at ~50 ms and ~150 ms. Source activation increase for the novel native word-forms at ~50 ms was underpinned by left-hemisphere IFG and posterior MTG regions in both conditions. Error bars denote SEM.  $p < 0.05^*$ .

The results demonstrate attention-independent neural enhancement to novel native word-forms at an early latency within a short ~30-minute exposure. Specifically, (1) the response showing the increase due to exposure was observed at a remarkably early latency at ~50 ms after the lexical status of the word-form could be identified; (2) this response increase was significant only for the novel word-forms with native phonology; (3) the neural enhancement was similar in both ignore and attend conditions, showing no interaction with attention modulation; and (4) the neural enhancement was underpinned by source activation in left inferior frontal and posterior temporal cortex. Corroborating such early latency of rapid lexicalisation effects, the earliest response distinguishing the lexical status of spoken word-forms was previously discovered at 50 ms (MacGregor et al., 2012), and a recent study suggested even earlier (30 ms post DP) first-pass lexical processing (Shtyrov & Lenzen, 2017). Importantly, the neural increase for novel words negated the brain's usual reaction to repetition, i.e. suppression of response (Grill-Spector et al., 2006). Critically, the response did not increase but decreased to known words. This is in line with findings including other modalities showing repetition suppression for familiar but enhancement for unfamiliar stimuli that, nevertheless, have a neural circuit they can be mapped onto (Henson et al., 2000; Gagnepain et al., 2008). Such general pre-requisite for neural learning would explain why the neural increment to the novel word-forms with unfamiliar phonology was not as substantial as for novel native forms with the time-frame and number of repetitions in the current study. The automatic nature of the response enhancement, taking place irrespective of focussed attention on the spoken stimuli, echoes previous results of novel word learning from attended speech streams. Greater activity change in the perisylvian cortex distinguished the word learning conditions even if subjects were unable to explicitly indicate whether they had been exposed to words or random syllable combinations (McNealy et al., 2006). It seems that in spite of the specific context of novel word exposure, such neural learning process is hardly a conscious one.

The neural sources underlying the sensor-level enhancement were also consistent across the two conditions: Activity increase in inferior frontal and posterior temporal source locations in the left hemisphere were found to correspond to response increase to novel native word-forms. These areas are part of the speech network of the brain in terms of both structure (Catani et al., 2005; Glasser & Rilling, 2008) and function

(Hickok et al., 2007; Saur et al., 2008). The source locations show correspondence with those observed in word learning studies employing different kinds of learning tasks: Activation enhancement in left-lateralised temporo-parietal gyrus and posterior IFG were observed in paired-associate and list learning (Paulesu et al., 2009). Furthermore, the strength of anatomical functional connections between the posterior temporal and inferior frontal areas were shown to correlate with word learning performance (López-Barroso et al., 2013). Most importantly, the result is in line with previous similar studies that demonstrated rapid neural learning dynamics for novel word-forms under ignored exposure (Shtyrov et al., 2010b; Shtyrov, 2011; Yue et al., 2014).

The second response at ~150 ms showed different dynamics than the first one. Namely, for all word types the response attenuated between the early and late stages of exposure invariably of condition. Attention, however, had an effect on response magnitudes between word types such that the responses to attended novel non-native word-forms were smaller compared to the native items while in the ignore condition response magnitudes did not differ between any word types. This attention effect contrasts the typical finding of pseudo-words eliciting larger responses at 120-150 ms than known words in attended conditions (Garagnani et al., 2009; Shtyrov et al., 2010a). However, the pseudo-word > known word effect has been found with native items, and a trend towards the novel native word-form response being greater than the known word one in the attend condition was observed here as well.

#### **4.2.2 MEMORY PERFORMANCE FOR WORDS**

Behavioural performance in the memory tests (Table 4) manifested a significant Task  $\times$  Lexicality interaction for HR ( $F(1,21) = 8.85, p = 0.007$ ) whereby the overall hit rate was higher in the recognition than free recall task ( $p < 0.001$ ) and known words were remembered better than pseudo-words ( $p < 0.018$ ). Hit rate after attend condition was better than after ignore condition, shown by a significant main effect ( $p < 0.001$ ).

In the free recall task, a significant Lexicality  $\times$  Validity of response interaction ( $F(1,21) = 21.48, p < 0.001$ ) demonstrated higher number of correct recalls of known words than pseudo-words ( $p < 0.001$ ) whereas there was no significant difference for incorrect responses ( $p = 0.08$ ). There was a higher number of correct than incorrect

responses for known words ( $p = 0.003$ ) but vice versa for pseudo-words ( $p = 0.005$ ). Overall, more items were recalled in the attend compared to the ignore condition ( $p < 0.001$ ).

In the recognition task, the validity of the response (HR vs. FA) had a significant interaction with lexicality ( $F(1,21) = 8.54$ ,  $p = 0.008$ ) and attention ( $F(1,21) = 29.26$ ,  $p < 0.001$ ). Overall, HR was higher than FA ( $p < 0.001$ ). Unlike HR, FA did not differ between word types ( $p = 0.673$ ). HR was significantly higher in attend than ignore condition ( $p < 0.001$ ), whereas FA did not differ between the conditions ( $p > 0.73$ ). Discriminability analysis ( $d'$ ) showed higher discriminability for known over pseudo-words ( $F(1,21) = 9.10$ ,  $p = 0.007$ ) and for attended vs. ignored input ( $F(1,21) = 22.27$ ,  $p < 0.001$ ).

**Table 4.** The mean number of correct and incorrect responses and the corresponding hit rate (HR), false alarm rate (FA), and discriminability value ( $d'$ ) in the memory tasks in ignore (first row) and attend (second row) conditions. SEM in brackets.

		Correct	Incorrect	HR (%)	FA (%)	$d'$
Novel native word-forms	Free recall	0.23 (0.09)	0.95 (0.23)	5 (1.83)	NA	NA
		1.73 (0.26)	3.27 (0.54)	35 (5.29)	NA	NA
	Recognition	1.86 (0.23)	1.45 (0.32)	39 (4.12)	16 (2.83)	0.76 (0.13)
		3.59 (0.26)	1.09 (0.27)	69 (4.43)	13 (2.29)	1.81 (0.16)
Known words	Free recall	1.50 (0.22)	0.45 (0.16)	30 (4.31)	NA	NA
		3.32 (0.23)	2.05 (0.45)	66 (4.63)	NA	NA
	Recognition	2.55 (0.25)	0.91 (0.24)	50 (4.86)	11 (1.98)	1.33 (0.19)
		4.32 (0.20)	1.45 (0.23)	80 (3.12)	15 (2.10)	2.04 (0.15)

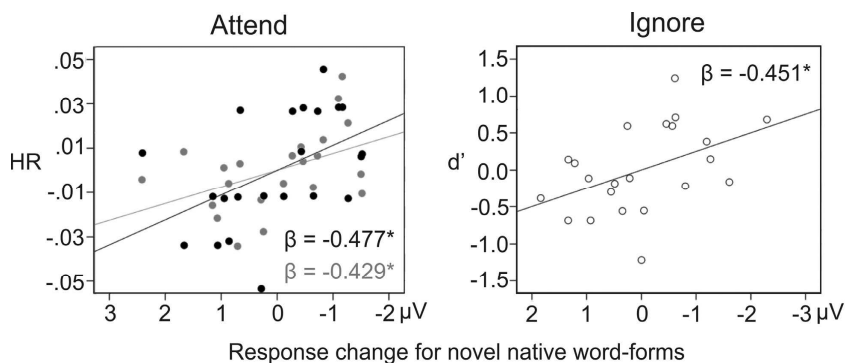
Comparison of correct responses for the film questionnaire validated that subjects had paid attention to the instructed modality, i.e. the mean score in the attend condition (12.27, SEM = 0.25) was significantly higher than in the ignore condition (6.23, SEM = 0.84) out of the fifteen questions ( $t(21) = 7.57$ ,  $p < 0.001$ ).

The behavioural memory results show an unsurprising pattern of better recall and recognition of known over newly learnt words after both conditions, and further, better overall memory in the attend than ignore condition. Hit rates exceeded chance level for the recognition of attended novel native words (conforming with Toro et al., 2005), as well as for attended known words in both memory tasks. The drawback of the memory tasks used is that learning of the novel non-native tokens could not be tested. However, since false alarms in the recognition task did not significantly differ between the native word types or conditions, the possible interference of the non-native items

did not evidently influence the results. In future studies, results on non-native word-form learning could be attained by employing an auditory recognition task.

#### 4.2.3 ASSOCIATION OF NEURAL MEMORY-TRACE BUILD-UP AND BEHAVIOURAL MEMORY

The neural responses at ~50 ms, suggested to reflect neural learning of novel native word-forms, were set to predict how well they were remembered behaviourally (Fig. 6). Indeed, the neural response increase to *attended* novel native word-forms significantly predicted their subsequent recognition ( $\beta = -0.477$ ,  $p = 0.032$ ,  $R^2$  change = 0.22). This neural change also predicted the free recall of words overall in the attend condition ( $\beta = -0.429$ ,  $p = 0.04$ ,  $R^2$  change = 0.178). Moreover, the neural enhancement to *ignored* novel native word-forms predicted their discriminability in the recognition task ( $\beta = -0.451$ ,  $p = 0.039$ ,  $R^2$  change = 0.199). These results indicate that neural dynamics elicited by the exposure to novel words is significantly associated with their subsequent memory at the behavioural level. Age alone did not significantly predict behavioural memory in any of the regression models.



**Figure 6.** Linear association between individual response change to novel native word-forms and hit rate (HR) for overall free recall (grey dots) as well as recognition of novel native word-forms (black dots) in attend condition, and discriminability ( $d'$ ) of the corresponding ignored novel words (white dots). Values are standardised scores.  $p < 0.05^*$ .

Importantly, the significant associations between the neural response increment to novel native word-forms and the consecutive behavioural memory verify the presumption of the neural response dynamics to reflect word learning, which was not previously tested (Shtyrov, et al., 2010b; Shtyrov, 2011). While the neural response

increase to attended novel native word-forms specifically predicted their recognition, it also predicted the free recall over word types. Furthermore, stronger response enhancement to ignored novel native items predicted their behavioural discriminability after exposure, further validating the suggestion that the neural dynamics specifically represents memory-trace formation even in the absence of focussed attention. These results refer to the specificity of the relationship in the case of recognition memory and generality in more effortful retrieval. The neural dynamics found here is suggested to manifest automatic rapid plasticity in the neocortex for word learning.

### **4.3 STUDY III: INFLUENCE OF LANGUAGE LEARNING EXPERIENCE ON MEMORY-TRACE FORMATION FOR NOVEL WORDS**

#### **4.3.1 RESPONSE CHANGE VARIABILITY TO NOVEL WORD-FORMS WITH DIFFERENT PHONOLOGY**

STUDY III exploited the ERP data obtained in STUDY II and scrutinised links between individual language learning experience and neural memory-trace build-up. Specifically, the dynamics of the learning-related response at ~50 ms during exposure to both novel native and non-native word-forms was analysed for associations with various measures of language experience (Table 5). Although the response increased to both novel word types, the inter-individual variance in the response enhancement to novel *non-native* word-forms was greater than for novel *native* word-forms, and hence the response enhancement did not reach significance for non-native items (see results of STUDY II). Mean response increase to non-native items across conditions was 0.24  $\mu\text{V}$  (SEM = 0.30 in ignore and 0.34 in attend condition). Mean response increase to novel native material was 0.22  $\mu\text{V}$  (0.23) in the ignore and 0.41  $\mu\text{V}$  (0.24) in the attend condition, and F-test of across condition variances of the novel non-native and native word-forms demonstrated a significant difference ( $p = 0.026$ ).

### 4.3.2 RELATIONSHIP BETWEEN LANGUAGE EXPERIENCE AND LEARNING-RELATED NEURAL DYNAMICS

Measures of language experience acquired from the subjects are presented in Table 5. Details on the specific languages the subjects had learnt are displayed in Table 6. Subjects had learnt at least two foreign languages, as is standard in the Finnish school system. English was primarily the first non-native language that was learnt (86 %), and two subjects had been exposed to a language other than their native one before school onset in their neighbourhood (which had not, however, led to substantial nor proficient use of that language before language studies in school).

**Table 5.** Subjects' learning history of non-native languages in Study III. Proficiency levels were estimated with a scale 1-5 (1 = basic, 5 = excellent).

	Mean (SD)	Range
Number of learnt non-native languages	3.32 (1.04)	2-5
Average age of acquisition (AoA)	11.84 (1.66)	9-14.6
Average time since AoA (years)	12.25 (3.36)	7.33-17.33
Average self-reported proficiency	3.13 (0.68)	2-3.67

A significant negative correlation between AoA and proficiency ( $r = -0.745$ ,  $p = 0.013$ ) in the reported languages indicated that the earlier the learning onset, the higher the achieved proficiency.

**Table 6.** The reported non-native languages and the percentage of subjects with a learning history in the language. Mean (SD) of AoA, years since AoA, and proficiency for each language.

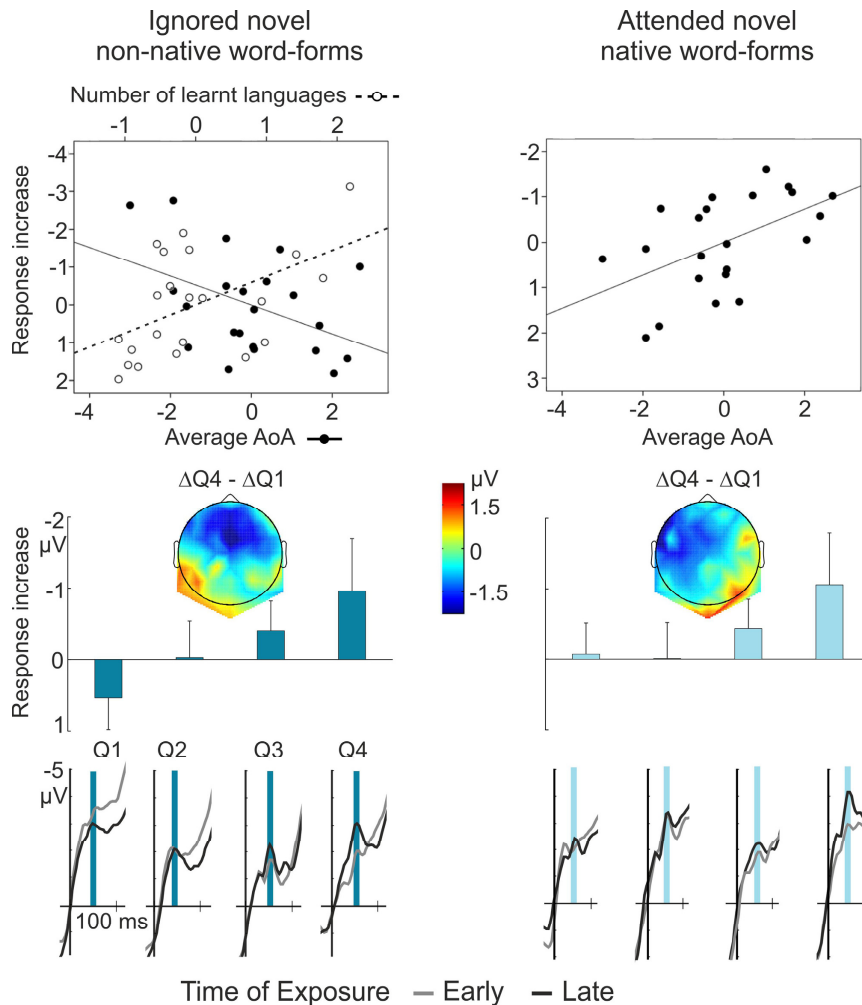
	Percentage of learners	AoA	Years since AoA	Proficiency
English	100	9.27 (1.42)	14.82 (4.48)	4.32 (0.72)
Swedish	100	11.59 (3.08)	12.5 (4.04)	3.05 (1.09)
German	50	11.82 (2.6)	11.91 (4.13)	2.64 (1.12)
French	32	13.17 (2.04)	12.67 (5.05)	2.33 (1.03)
Spanish	23	16.2 (3.56)	6.6 (1.67)	2.2 (1.64)
Danish	9	19 (0)	2 (0)	1 (0)
Latin	5	17 (0)	12 (0)	3 (0)
Greek	5	22 (0)	7 (0)	2 (0)
Japanese	5	20.5 (4.95)	6 (2.83)	1 (0)
Korean	5	23 (0)	2 (0)	2 (0)

Since age did not correlate with the neural response changes ( $p$ -values  $> 0.11$ ), it was not added into the regression models as a predictor. Separate multiple linear



regressions for neural changes to novel native and non-native word-forms showed significant relationships for two measures of language experience. Namely, a significant regression model ( $F(2,19) = 3.87, p = 0.039, R^2 = 0.289$ ) showed that the response increase to *ignored novel non-native word-forms* was significantly predicted by the number of learnt languages ( $B = -0.748, p = 0.019$ ) and average AoA ( $B = 0.381, p = 0.05$ ). That is, more learnt languages with an earlier average age of acquisition predicted greater response increase (Fig. 7 left). The same model approached significance for attended non-native items ( $F(2,19) = 3.05, p = 0.071, R^2 = 0.243$ ) where both the number of learnt languages ( $B = -0.838, p = 0.024$ ) and the average AoA ( $B = 0.268, p > 0.2$ ) had coefficient effects similar to the model in ignore condition.

Further, a significant regression model for response increase to *attended novel native word-forms* ( $F(2,19) = 4.79, p = 0.021, R^2 = 0.335$ ) revealed that average AoA significantly predicted the neural increase ( $B = -0.364, p = 0.016$ ) such that the later the learning of foreign languages had started, greater was the response increase (Fig. 7 right). The number of languages was not a significant predictor here ( $p > 0.7$ ). In the models for attended non-native vs. native word-forms, the weights of predictors differed significantly (number of learnt languages  $z = -2.514, p = 0.032$ ; and average AoA  $z = -2.508, p = 0.012$ ).



**Figure 7.** Significant multiple linear regressions for the response increase to ignored novel non-native word-forms (left) and attended novel native word-forms (right) with the number of learnt non-native languages and their average AoA as predictors. The partial plots (top) show significant predictors of the response enhancement (standardised values). The middle and bottom panels show the neural response data divided in quartiles according to the significant predictor measures (absolute amplitude change and response curves at early and late stages of exposure per quartile, respectively). Scalp topographies demonstrate the difference between the response changes of the first and last quartiles.

In sum, the efficiency of the response enhancement to novel word-forms during exposure was found to be associated with language experience, namely, the number of learnt non-native languages and their average age of acquisition. Critically, the effects were manifested by native speakers of a single language and not by early bilinguals. The relatively notable variation in the number of learnt languages and the

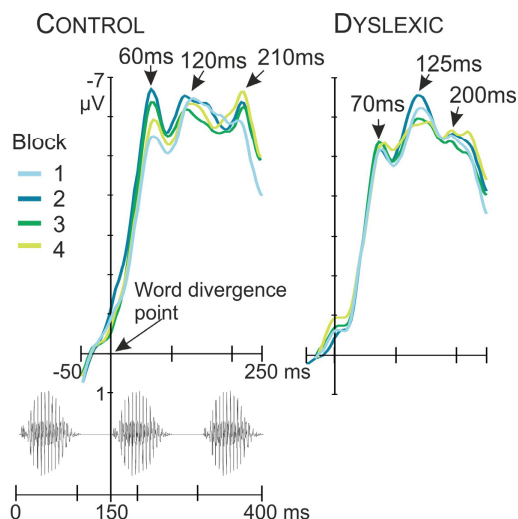
rather high average learning onsets, ranging from 9 to over 14 years of age, serving as significant predictors of neural learning of word with yet novel phonology, imply that influential plastic changes take place in late childhood and onwards. Higher number of previously learnt languages combined with earlier average AoA was associated with greater response enhancement to novel non-native items. This predictive model was significant for the neural dynamics to ignored non-native words and close to significant to the attended ones. This refers to an automatic influence of the existing neural network of acquired non-native languages to repeatedly perceived novel non-native speech material in the absence of controlled attention. The result supports behavioural findings suggesting that bi- and multilinguals are better able to acquire words of a new language than monolingual speakers (Papagno & Vallar, 1995; Van Hell & Mahn, 1997; Kaushanskaya & Marian, 2009a, 2009b).

Interestingly, the effect of language experience on neural learning was not restricted to novel non-native input: Higher average AoA of learnt non-native languages alone was associated with greater response increase to novel native word-forms. This suggests that native language learning is modulated by how early in life the neural language network has been exposed to non-native languages. The effect was established only in the attend and not in the ignore condition, which implies an interaction of attention allocation and the phonological familiarity of the repeated word to reflect differential input from the existing network on the processing of novel native vs. non-native material. Furthermore, the scalp topography of the difference in response increase between the quartile groups of individuals with earliest and latest average AoA of foreign languages (Fig. 7 middle left) implies stronger left-lateralisation of the origins giving rise to the response increase to novel native words in the group with late AoA. Although the finding that learning foreign languages has an impact on the learning of native language is novel and thus should be considered with caution and requires replication, the recruitment of overlapping brain regions during the processing of native and non-native languages has been widely shown (for reviews, see Perani & Abutalebi, 2005; Higby et al., 2013). A considerable contribution of AoA in determining the degree of co-activation between L1 and L2 is typically found (Perani et al., 1998; De Bleser et al., 2003; Briellmann et al., 2004; Tatsuno & Sakai, 2005; Bloch et al., 2009). As for the number of learnt languages, the current study provides novel neural evidence of its influence on further word learning.

## **4.4 STUDY IV: RAPID WORD MEMORY-TRACE BUILD-UP IN FLUENT-READING AND DYSLEXIC CHILDREN**

### **4.4.1 NEURAL RESPONSE DYNAMICS TO NOVEL SPOKEN WORD-FORMS**

Three distinct negative responses taking place after DP and before the spoken word offset were detected in both groups (Fig. 8). Previous results of the first negative response after DP showing the exposure-related increase (Shtyrov et al., 2010b; Shtyrov, 2011) guided the analysis to primarily focus on the first negative response. The latency of the first peak was 63 ms (SEM = 2.14) in the control and 69 ms (SEM = 2.28) in the dyslexic group. This latency difference was significant ( $F(1,40) = 6.45$ ,  $p = 0.015$ ) referring to a delay in the critical spoken input processing in the dyslexic group. Crucially, the neural dynamics of the response amplitude during exposure was different between the groups, exhibited by a significant interaction of Group  $\times$  ROI  $\times$  Block  $\times$  Sub-block ( $F(1,40) = 4.22$ ,  $p = 0.047$ ). Post hoc pairwise comparisons revealed this interaction to derive from a significant response increase between the first two blocks in the first half of exposure in the control group ( $p = 0.007$ ; Fig. 9 top) while in the dyslexic group the response showed no change during the entire exposure ( $p$ -values  $> 0.6$ ). The magnitude of the response in the second sub-block was also greater in the control than dyslexic group ( $p = 0.037$ ). The topographical distribution showed more pronounced responses in the midline ROI compared to the left and right hemisphere ones across groups ( $F(2,80) = 3.47$ ,  $p = 0.036$ ) in all blocks ( $p$ -values  $< 0.001$ ). Follow-up analysis of the midline distribution further displayed stronger responses in the anterior than the posterior region ( $F(1,40) = 224.78$ ,  $p < 0.001$ ).



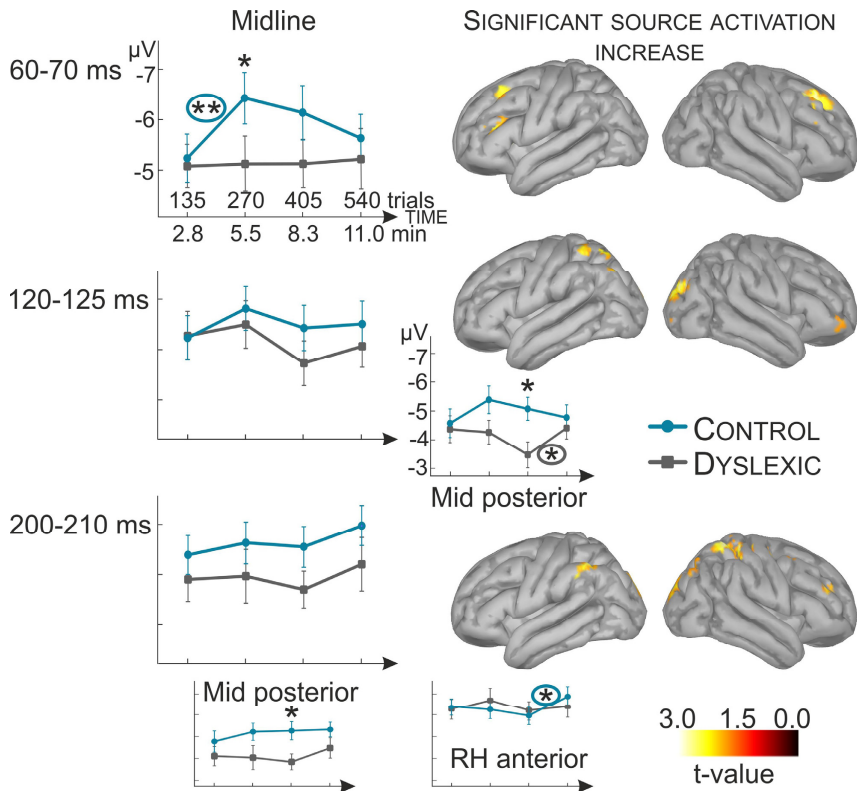
**Figure 8.** Responses to the novel word-form in controls and dyslexics. Different colours of curves indicate the average curve in each consecutive block. The stimulus elicited three prominent negative peaks after DP. The audio waveform shows the temporal continuum of the spoken stimulus aligned to the ERP.

The second peak occurred ~50-60 ms later, at 122 ms (SEM = 3.47) in the control and 125 ms (SEM = 3.44) in the dyslexic group (latency difference n.s.). The response was strongest in the midline ROI ( $F(2,80) = 78.82, p < 0.001$ ) and was generally stronger in the anterior than posterior sites ( $F(1,40) = 133.45, p < 0.001$ ). The midline ROI follow-up analysis resulted in a significant interaction of Group  $\times$  Block  $\times$  Sub-block  $\times$  Anterior-posterior ( $F(1,40) = 12.11, p = 0.001$ ) which indicated a significant response amplitude increase between the blocks within the second half in the posterior region in the dyslexic group ( $p = 0.029$ ; Fig. 9 middle). Moreover, the response in the beginning of the second half in this area was smaller in the dyslexic than the control group ( $p = 0.011$ ). No significant difference was found for the adjacent blocks between the first and second half in a supplementary t-test. This confirmed that the change in response dynamics in the dyslexic group was established at the later part of exposure.

The third response was elicited 40-50 ms before the stimulus offset, at 210 ms (SEM = 5.11) in the controls and 199 ms (SEM = 4.57) in the dyslexics (difference n.s.). These latencies correspond to 49-60 ms after the final syllable onset, and thus the response possibly reflects the final stages of analysis of the stimulus. ROI main effect ( $F(2,80) = 104.24, p < 0.001$ ) indicated that responses were greater at the midline and right-hemispheric ROIs than over the left hemisphere ( $p$ -values  $< 0.045$ ).

In both ROIs, the responses were stronger in the anterior than posterior electrode sites ( $F(1,40) > 158$ ,  $p < 0.001$ ). Topographical follow-up of the two dominant ROIs showed significant four-way interactions. In the RH ROI, this interaction ( $F(1,40) = 6.05$ ,  $p = 0.018$ ) derived from significant response enhancement in the anterior region during the second half of exposure in the controls ( $p = 0.029$ ; Fig. 9 bottom). The same interaction in the midline ROI ( $F(1,40) = 4.34$ ,  $p = 0.044$ ) was explained by the response of the first block of the second half in the posterior site being stronger in the controls than dyslexics ( $p = 0.013$ ).

The cortical source activity changes underlying the significant sensor-level response dynamics (Fig. 9) of the first response in controls revealed activity increase ( $t(19) = 2.26$ ,  $p = 0.018$ ) in the left frontal sulcus (Talairach coordinates  $x = -38$ ,  $y = 29$ ,  $y = 17$ ), just adjacent to MFG (BA46) and LIFG (BA44), and in superior frontal gyri (SFG BA8  $x = -22/23$ ,  $y = 29/30$ ,  $z = 45/43$ ) bilaterally ( $t(19) > 2.1$ ,  $p < 0.025$ ). The significant response increase in the later stage of exposure in dyslexics was generated by source activation increase in the left superior parietal cortex (SPL BA7  $x = -38$ ,  $y = -50$ ,  $z = 59$ ;  $t(19) = 2.06$ ,  $p = 0.027$ ) and the right occipital cortex (BA19  $x = 24$ ,  $y = -87$ ,  $z = 29$ ;  $t(19) = 2.67$ ,  $p = 0.008$ ). In addition to these, a small activity increase was detected at the right anterior prefrontal cortex (BA10  $x = 44$ ,  $y = 54$ ,  $z = -6$ ;  $t(19) = 1.78$ ,  $p = 0.05$ ). The response increase in controls late in exposure was underpinned by sources in the right prefrontal cortex (BA9  $x = 33$ ,  $y = 43$ ,  $z = 26$ ;  $t(19) = 2.55$ ,  $p = 0.01$ ) and superior parietal lobe (BA7  $x = 34$ ,  $y = -39$ ,  $z = 65$ ;  $t(19) = 2.87$ ,  $p = 0.005$ ), as well as in the left angular gyrus (BA39  $x = -47$ ,  $y = -53$ ,  $z = 51$ ;  $t(19) = 2.53$ ,  $p = 0.01$ ).



**Figure 9.** Response dynamics of each deflection in the control and dyslexic groups. Average response amplitudes per group are shown in each of the four blocks with the number of trials and time passed until the end of each block marked on the x-axis. Significant response increases between blocks are marked with circled asterisks (changes in controls marked in blue and in dyslexics marked with grey), and the corresponding cortical source activations underlying the changes are superimposed on an age-appropriate MRI. Asterisks without circles denote significant difference in response amplitude between the groups in the block. Error bars signify SEM.  $p < 0.01^{**}$ ,  $0.05^{*}$ .

Taken together, the neural response pattern that was elicited by the novel word-form over the course of 540 repetitions was considerably different in the two groups of children. Crucially, control children had similar response dynamics to that observed in corresponding passive oddball paradigms in adults (Shtyrov et al., 2010b; Shtyrov, 2011) with the earliest response after DP showing the rapid exposure-related response increase. The neural enhancement was established within the first 6 minutes of exposure to the frequent token, which is even faster than previously shown for adults (15-30 minutes). Yet, the number of repetitions (136-270) within which the greater amplitude was established overlaps with the number of trials (150-160) of the adult studies. Furthermore, the response latency at 60 ms in controls aligns well with the

one observed in response to words with a CVCV structure in adults in STUDY II. Albeit the current study lacked a memory task to account for the behavioural recall and recognition of the novel word-form later on, given the characteristics of the response fitting that of the adult studies, these response dynamics are likely to represent neural memory-trace formation for the novel word-form. The neural source activation underlying the exposure-related response increase, however, was partially different from the sources found in adults: While a clearly left-lateralised fronto-temporal activation enhancement was observed in adults (Shtyrov et al., 2010b; Shtyrov, 2011; STUDY II), the children recruited the prefrontal cortex bilaterally. The left inferior frontal source was observed only in the left hemisphere whereas the superior frontal DLPFC source enhancement was elicited symmetrically across the hemispheres. The only previous study examining the neural bases for spoken word learning in children found that after implicit parsing of novel words from attended speech streams, listening to words that had been repeated in the stream, compared to totally novel words or those with only one occurrence, activated the left IFG (McNealy et al., 2010). Further, during the exposure to speech streams with recurring new words, adults exhibited more temporal involvement than children, and children showed more bilateral activation. These findings align with those observed here and in STUDY II, with the temporal recruitment found in adults missing in children and children showing bilateral frontal activation as opposed to the left-lateralised fronto-temporal activity in adults.

Compared to the control group, the first response in the dyslexics was significantly delayed in latency which is in line with the findings of delayed early phonological processing in spoken word recognition in dyslexia (Metsala, 1997; Bonte & Blomert, 2004; Bonte et al., 2007). Strikingly, the dyslexics exhibited no changes in the amplitude of this response throughout the entire 11-minute exposure. Such lack of response change, even with extended number of repetitions compared to the controls, suggests a severe impairment in the initial novel phonological word-form encoding in dyslexic children. The result implies that dyslexics do not benefit from extensive passive exposure to words, at least to those with no given meaning. This phonological word-form impairment is possibly behind the novel word learning difficulty shown with associative word learning regimes (Vellutino et al., 1975, 1995; Aguiar & Brady, 1991; Mayringer & Wimmer, 2000; Messbauer & de Jong, 2003; Di Betta et al., 2006;



Li et al., 2009; Howland et al., 2013; Litt & Nation, 2014). Moreover, the current result is in line with the ‘anchoring deficit’ theory whereby failure in ‘anchoring’ the presented stimuli and analysing consecutive stimuli relative to this referent is behind a more general learning difficulty in dyslexia (Ahissar et al., 2006; Ahissar, 2007; Oganian & Ahissar, 2012).

The later ERPs demonstrated further discrepancies between the groups. The response elicited at the posterior area at ~125 ms increased significantly in the final half of exposure in dyslexics. The topographical as well as source-level occipital and superior parietal location of this enhancement can hardly be explained by cortical activation critical for spoken word perception. The enhancement could be related to alternative processing routes for word-forms such as mental imagery or visual systems in dyslexia (Flynn et al., 1992; Pugh et al., 2001). Curiously, the third response at ~200-210 ms, occurring just ~50 ms before word offset, showed a response increase at the final half of exposure in controls. Originating in the right anterior area with DLPFC and superior parietal sources, as well as left angular gyrus activation, this enhancement might reflect re-analysis of the word information (Friederici, 2002; MacGregor et al., 2012). This frontal response increase was again missing in the dyslexic group.

#### **4.4.2 RELATIONSHIP OF LITERACY SKILLS AND NEURAL MEMORY-TRACE FORMATION DYNAMICS**

Results of the dyslexic subjects in the neuropsychological tests were in accordance with typical performance in developmental dyslexia (Denckla & Rudel, 1976; Bruck, 1992; Korkman et al., 2008; Pennala et al., 2010), with significantly lower scores compared to controls in verbal tasks, including verbal reasoning, phonological processing, verbal short-term, working, and long-term memory, rapid naming tasks while perceptual reasoning did not differ between groups (Table 7). Tests of reading fluency and writing accuracy confirmed significant deficits in the dyslexic group with mean standardised scores < 1.6 SD in reading and < 1 SD in writing. Average performance of the control group was at or slightly above 1 SD of the normative average level in all tests.

**Table 7.** Mean scores (SD) of neuropsychological measures.

	<b>Controls</b> (n = 21)	<b>Dyslexics</b> (n = 21)	<b>t / F</b>	<b>p-value</b>
<b>Age</b>	10.69 (0.98)	11.23 (1.09)	1.70	0.098
<b>PRI</b>	111.62 (10.50)	108.90 (11.38)	0.65	0.427
Block design	11.81 (2.42)	11.00 (2.98)	0.93	0.340
Picture concepts	11.71 (2.49)	11.86 (2.39)	0.04	0.851
Matrix reasoning	11.71 (2.00)	11.19 (2.56)	0.55	0.465
<b>Similarities</b>	12.14 (1.74)	9.52 (2.23)	18.03	< 0.001***
<b>WMI</b>	104.71 (10.92)	96.86 (11.64)	5.09	0.030*
Digit span	10.14 (2.69)	9.52 (2.52)	0.59	0.446
Letter-number sequencing	11.33 (1.83)	9.43 (2.46)	8.11	0.007**
<b>Word list interference</b>	9.62(2.52)	8.29 (2.35)	3.15	0.084
<b>Memory for names</b>	10.76 (2.79)	8.48 (2.06)	9.10	0.004**
Immediate recall	10.52 (2.93)	8.71 (2.12)	5.26	0.027*
Delayed recall	11.33 (3.04)	8.43 (2.23)	12.49	0.001**
<b>Phonological processing</b>	12.05 (1.72)	8.19 (3.01)	26.01	< 0.001***
<b>RAN errors†</b>	5.19 (4.01)	6.52 (4.25)	3.12	0.056
speed (s)†	142.10 (19.05)	162.10 (18.80)	5.86	0.006**
<b>RAS errors‡</b>	2.33 (2.11)	3.71 (2.26)	2.08	0.138
speed (s)‡	69.10 (11.31)	83.24 (12.45)	8.02	0.001***
<b>Reading fluency</b> (correctly read words in 2 mins)				
raw score (max = 105)	97.10 (9.32)	66.52 (18.74)	41.84	< 0.001***
standardised score	11.86 (1.46)	4.86 (3.02)		
<b>Writing accuracy</b> (writing from dictation)				
raw score	31.24 (7.19)	36.48 (11.54)	13.04	< 0.001***
standardised score	11.33 (1.77)	6.67 (3.41)		

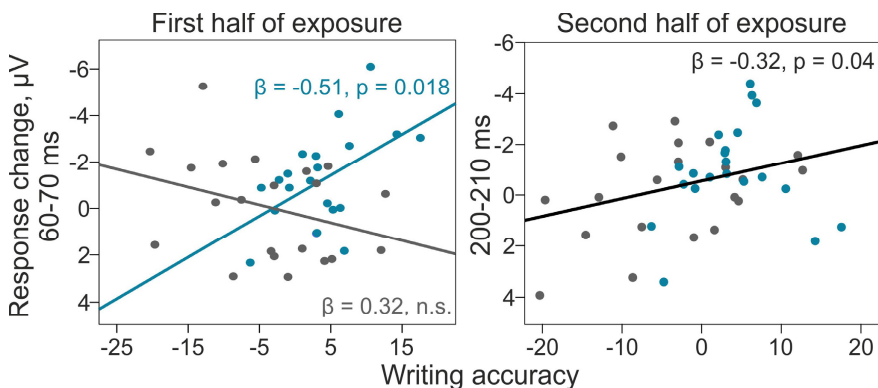
Normative standardised scores (mean = 10, SD = 3) are reported for the subtests of WISC-IV comprising Perceptual Reasoning Index (PRI) and Working Memory Index (WMI), verbal reasoning (Similarities) and NEPSY-II (Word List Interference, Memory For Names and Phonological Processing). T-statistic is reported for the age comparison, and F-statistic for the neuropsychological tests. P-values are Bonferroni-corrected. p < 0.05\*, 0.01\*\*, 0.001\*\*\*.

† Sum of 4 subtests (Colours, Numbers, Letters, and Objects).

‡ Sum of 2 subtests (Letters-Numbers, Colours-Numbers-Letters).

The linear regressions of age-corrected literacy measures (reading fluency and writing from dictation) and significant sensor-level response changes showed significant relationships between writing accuracy and the responses that showed significant increase in control subjects. Namely, only in the control group, better writing was significantly associated with greater response increase at 60 ms within the first half of exposure ( $F(1,19) = 6.76$ ,  $R^2 = 0.26$ ,  $\beta = -0.51$ ,  $p = 0.018$ ; Fig. 10 left). In

dyslexics, writing did not show a significant association with this response dynamics ( $F(1,19) = 2.20$ ,  $\beta = 0.32$ ,  $p = 0.16$ ). The difference between the regression coefficients of the groups was significant, indicated by univariate ANOVA interaction Group  $\times$  Writing accuracy ( $F(1,38) = 8.14$ ,  $p = 0.007$ ). There was a weak non-significant association between reading fluency and the response increment across groups at this latency ( $F(1,40) = 1.78$ ,  $\beta = -0.206$ ,  $p = 0.19$ ). Furthermore, better writing accuracy significantly predicted the third response increase at 200-210 ms in the right anterior ROI within the final half of exposure across groups ( $F(1,40) = 4.40$ ,  $R^2 = 0.10$ ,  $\beta = -0.32$ ,  $p = 0.042$ ; Fig. 10 right).



**Figure 10.** Associations between writing accuracy (age-corrected residual score) and neural dynamics. Better writing predicted greater response increment at 60 ms in controls (blue) within first half of exposure whereas dyslexics (grey) exhibited no such association (left). Within the second half of exposure, writing performance significantly predicted the third response at 200-210 ms across groups (right). Standardised values are presented.

In conclusion, literacy had significant associations with two of the observed response increments. Greater enhancement in the first response, which putatively reflected memory-trace formation, was significantly associated with better writing accuracy in controls. No association was found in dyslexics, which may be at least partially due to reduced variability in their responses over time. Echoing this finding, Oganian & Ahissar (2012) found that performance in learning to discriminate tones and spoken syllables through repetition was significantly predicted by reading fluency in controls but not in dyslexics. On the other hand, reading ability was found to predict the phonological measures of paired-associate word learning across poor readers and normal reading individuals (Aguiar & Brady, 1991; Windfuhr & Snowling, 2001; Hulme et al., 2007). Here, the non-significant positive relationship between the

response change and reading fluency over groups refers to some, albeit weak, commonality between exposure-related learning and reading skill. The other frontally distributed response change at 200-210 ms, which was only significant in controls, was predicted by writing accuracy across groups. That is, larger increase in the third response within the final half of exposure was associated with better ability to write from dictation. These results hint that literacy skills, especially the ability to map perceived speech onto its orthographical form, are related to word memory-trace formation in both groups of children. Furthermore, the findings endorse the notion that reading and writing skills have associations with novel word learning ability.

## 5 GENERAL DISCUSSION

The studies in the current thesis investigated the rapid formation and activation of memory traces for spoken words under perceptual exposure using ERPs. The main findings were: (1) the frequency with which a word occurs in a language determined the magnitude of the early latency electrophysiological response to the spoken word once heard, which arguably reflects the activation strength of the lexical memory trace in the neocortex; (2) meaningless novel (pseudo) words that had not been encountered prior elicited a weak neural response, presumably due to the lack of pre-existing memory traces to these stimuli; (3) extensive repetitive perceptual exposure to such attended or ignored novel word-forms over a short period of time resulted in neural response enhancement that reached the magnitude of known word responses; (4) the significant response increase was specific to native but not non-native word-forms; however, (5) the efficiency with which the neural response increase occurred to these different types of novel words was related to previous learning of non-native languages, which had presumably shaped the neural language networks; and (6) while typically developing children showed exposure-related response dynamics to a novel word-form similarly to that in adults, such response modulation lacked altogether in dyslexic children during the short exposure, which might be related to the putatively compromised learning through stimulus repetition more generally in dyslexia.

### 5.1 MEMORY TRACES FOR WORDS IN THE DISTRIBUTED NEURAL LANGUAGE NETWORKS

The results of the current thesis on the whole are in accordance with the Hebbian learning framework for language (Pulvermüller, 1999). In STUDY I, greater magnitude of the response amplitude to words with higher compared to lower word frequency presumably indicated stronger ignition of the neural memory trace. This can be interpreted to demonstrate the end result of recurrent exposure, i.e. greater connection strength of the cell assembly evolved through a Hebbian learning process. STUDIES II and IV, on the other hand, can be argued to manifest the initial stages of Hebbian learning through a brief exposure period. Sufficient repetition of novel words, not

included in the pre-existing word memory network, led to an enhancement of the initially weak neural response. According to the Hebbian framework, the magnitude of the neural response to a spoken item reflected the activation strength of a memory circuit for the specific word-form. In the absence of such circuits to novel words initially, they elicited smaller responses (most likely generated by the mere acoustic-phonetic, rather than lexical, processing) than known words. Known words, on the other hand, activated their long-term memory circuits resulting in larger response amplitudes. Repetitive exposure to the novel items, however, strengthened the connections of the neurons activating for the novel acoustic-phonetic combinations (i.e. word-forms), leading to an increase in the response amplitude to the word-form. This process is suggested to represent memory-trace formation by way of Hebbian learning.

Furthermore, the results in this thesis can be largely accommodated by the Cohort model (Marslen-Wilson, 1987). Namely, in all studies, the native input (known and novel (pseudo) word-forms) created no bias at the first syllable, thus presumably activating the exact same cohort of words in STUDY II and all possible cohorts for each first syllable in STUDIES I (where the cohort sizes did not significantly differ between the two first syllables) and IV. This would imply that no difference in activation levels was present at the time of the first syllable. However, as the spoken input diverged at the second syllable onset from lexical competitors, the word-form could be isolated and the input activated existing memory circuits for words fully, denoting lexical access. Correspondingly, the activation created by the novel items decreased, reflected by the smaller responses to the pseudo-words in STUDY I and to the novel word-forms at the early stage of exposure in STUDIES II and IV.

The above description of response dynamics can also be accounted for by the Distributed cohort model (Gaskell & Marslen-Wilson, 1997), which endorses the notion of initially partial activation of neuronal circuits of the cohort items. The acoustic-phonetic overlap between the speech input and the lexical competitors elicits *partial* activation of the memory circuit of matching candidates and this activation increases for spoken words and abolishes for pseudo-words over the unfolding of the speech signal, leading to a fully-fledged activation of an existing word memory circuit. Through these activations in recurrence, the internal connection strength of the neural memory traces may be amplified. The rapid development of the response strength to

novel words observed in STUDIES II and IV, moreover, implies extraordinary speed in the initial development of such memory networks for speech.

The activation of known word memory representations and the effects of short exposure to unfamiliar words were manifested in the absence of focussed attention (as attention was directed to visual stimuli) or active controlled processing of the stimuli. This refers to automaticity of speech processing. It can be suggested that existing neural word memory traces, with form-specific acquired properties, are *per se* activated irrespective of the cognitive processes operating on them. Such automaticity was verified by STUDY II showing that the learning-related neural dynamics was similar regardless of different degrees of appointed attention on the stimuli.

While the proposed build-up of neural memory circuits was significantly associated with the subsequent recognition of the repeated native items at the individual level, confirming the neural dynamic pattern to actually represent learning of the novel words, the studies of this thesis cannot determine the long-term permanence of these memory traces. On a speculative note, as lexical integration has been shown to occur fast, without sleep-related consolidation (Lindsay & Gaskell, 2013; Coutanche & Thompson-Schill, 2014), it is possible that the intensive perceptual exposure employed in the studies of the current thesis is sufficient to show longer-term sustainability within the language circuitry. This should be further examined in future studies.

## **5.2 INFLUENCE OF LANGUAGE LEARNING EXPERIENCE AND READING ABILITY**

While such response enhancement to novel native words was significant within a brief exposure incorporating 150 repetitions of each token, this amount of exposure was not sufficient to generate significant enhancement to novel words with unfamiliar phonology across subjects. Crucially, however, factors of language experience were shown to be associated with the individual response dynamics to novel non-native word-forms in STUDY III. Namely, the number of previously learnt non-native languages and the average age at which learning of those languages had started, manifested two relationships to novel word learning. Firstly, the more languages had been learnt with earlier learning onsets, the more did the response for novel *non-native*

words increase. Secondly, the later the learning of the non-native languages had started, the greater the increase for novel *native* word-forms. The found effects of these factors of language experience on perceptual rapid learning are interpreted to support behavioural results of multilingualism posing more efficient non-native word learning (Papagno & Vallar, 1995; Van Hell et al., 1997; Kaushanskaya et al., 2009a, 2009b). Longitudinal evidence in early bilinguals points to such advantage on foreign language learning (Sanz, 2000). Strictly, the results of STUDY III cannot determine such causality. Rather, the results indicate a *co-existent association* between the background factors and the neural learning dynamics.

In accordance with the Hebbian memory-trace formation framework, the found relationship between language experience and novel word learning may index the individual variability of the neural language network for which novel traces are mapped onto. Indeed, when exposed to multiple foreign languages recurrently, new memory traces are formed and, on the other hand, the native word memory traces are presumably being partially activated in contexts of words that, in addition to familiar speech sounds, carry unfamiliar phonology as well. This may mean that the native memory traces have connections to the non-native ones, supported by accumulating evidence of native and non-native language processing recruiting largely shared brain areas (e.g. Perani et al., 1998; De Bleser et al., 2003; Briellmann et al., 2004; Tatsuno & Sakai, 2005).

The rapid memory-trace formation was, however, shown in adults and children with normal reading ability. The lack of this dynamic neural pattern in dyslexic children may originate from impaired capacity to benefit from repetition in learning (Ahissar et al., 2006; Szmalec et al., 2011). The result of STUDY IV is the first to show novel word learning impairment in dyslexia without semantic processing requirements (as in paired-associate paradigms; e.g. Aguiar & Brady, 1991; Messbauer & de Jong, 2003; Litt & Nation, 2014) or demands of serial order segmentation and regularity extraction (as in Szmalec et al., 2011; Oganian & Ahissar, 2012). Moreover, the impaired learning-related neural dynamics was found using a paradigm that did not impose preconditions for subtle speech contrast discrimination, which many studies have shown to be aberrant in dyslexia (Serniclaes et al., 2001; Bonte & Blomert, 2004; Goswami et al., 2011): The presented stimulus embedded three identical syllables, eliminating possible confusion in discriminating the acoustic-phonetic features of the



successive syllables from each other. Finally, one essential benefit of the paradigm was that no focussed attention on or other cognitive processing of the stimuli were assigned, in order to exclude their influence on the learning effects between the groups. To further alleviate possible differences in attention allocation during exposure, the brevity of exposure (only 11 minutes) ensured that the ability to sustain attention on the self-selected cartoon for the exposure period created an unlikely confounding factor. At the same time, these considerations apply to the significant learning effect found in control children. The finding of normally reading children showing learning effects closely similar to adults during distracted passive listening provide further support to the automatic word learning account across development. In the only previous neuroimaging study investigating word learning in children during short exposure to speech (McNealy et al., 2010), passive listening to the stimuli was not distracted by a task engaging attention to another modality as in STUDY IV. Thus, the current results of typically developing children provide the first neural evidence of rapid automatic word learning dynamics in childhood.

### **5.3 NEOCORTICAL ORIGINS OF EXPOSURE-RELATED EFFECTS**

The cortical origins of the exposure-related effects in STUDIES I, II and IV were predominantly located in the left temporal and prefrontal cortices. Enhanced source activations for higher compared to lower frequent words in STUDY I were found in the left inferior frontal and anterior temporal cortex as well as a more dorsal part of the prefrontal cortex. In STUDIES II and IV, rapid learning effects for novel native word-forms were generated in the left posterior temporal and inferior frontal cortices in adults, and in the left inferior/middle frontal cortex as well as bilateral dorsolateral prefrontal cortex in children. It seems, therefore, that the left prefrontal cortex is particularly critical in the strengthening of word memory traces. Nonetheless, studies of lexical processing have consistently shown engagement of both inferior frontal and temporal areas in adults (Damasio et al., 1996; Gold & Buckner, 2002; Davis et al., 2009; Bozic et al., 2013). According to the dual-stream model of speech processing (Hickok & Poeppel, 2004, 2007), speech input feeds into ventral and dorsal pathways connecting the left posterior temporal and frontal cortices. The ventral stream in

particular connecting the areas of posterior MTG and IFG is considered to account for mapping the speech sound to meaning. The rapid learning effect in STUDY II originated from these areas, implicating that the novel word-forms might have been undergoing even some binding to existing semantic networks (Gaskell & Dumay, 2003; Raettig & Kotz, 2008). Furthermore, IFG has been suggested to specifically be involved in lexical retrieval (Thompson-Schill et al., 1999; Zhuang et al., 2011, 2012).

The left IFG/MFG and bilateral DLPFC activation increase observed in the children of STUDY IV are more difficult to accommodate due to the lack of neuroimaging studies of spoken word processing in children. Results from the learning study by McNealy et al. (2010) provide some support, as newly learnt words compared to pseudo-words exhibited greater activation of LIFG, as well as bilateral anterior cingulate gyrus. Interestingly, in STUDY I, high-frequent spoken words also activated the left dorsal prefrontal cortex in adults, showing some resemblance with the dorsal sources for short exposure effects in children. This may further incline to the necessity of the prefrontal cortex involvement in exposure-related memory-trace formation and strengthening of the lexical memory traces. The results of STUDY IV, hence, tentatively suggest reliance especially on frontal cortical function in rapid novel word encoding in the developing brain.

The neocortical involvement in STUDIES II and IV are in line with repetition priming and fast mapping studies showing rapid learning effects relying on neocortical function (Haist et al., 1991; Henson, 2001; Gagnepain et al., 2008; Sharon et al., 2011). The results of the current studies showing activation increases originating from cortical sources argue for the strong capacity of the neocortex to incorporate novel input to existing neural networks. The current results do not, however, directly inform about the extent of hippocampal engagement in the encoding process, since EEG ultimately measures the gross net activity of the electric currents of pyramidal cell populations, including those originating from both neocortical and deeper structures, such as the hippocampus.

Dynamics of the early neural response, suggested to pertain word encoding, was not established in the children with dyslexia, who demonstrated only later exposure effects originating from brain areas without a clear relation to speech processing. Thus, making conclusions on their relevance on novel word processing is not meaningful. However, the lack of enhanced frontal activation in response to repetitive exposure of

a phonological word-form in the dyslexics may be related to abnormal function of the left frontal cortex especially in processing of phonological material. For instance, increased difficulty in word rhyming was associated with greater activation of left inferior frontal and medial frontal gyrus in controls but this was not observed in dyslexic children (Cao et al., 2006). Atypical white matter pathways of the left perisylvian network, with terminations in LIFG, have been reported widely in dyslexia (e.g. Steinbrink et al., 2008; Rimrodt et al., 2010; for review, see Catani & Mesulam, 2008). A recent meta-analysis determined hypoactivation of the fronto-striatal circuitry in phonological processing in dyslexia (Hancock et al., 2017).

## **5.4 METHODOLOGICAL CONSIDERATIONS**

The rapid word learning results of the current thesis implicate that the absolute exposure time is not the key element, which enables the memory-trace formation, but rather the number of repetitions. In STUDY II, the number of trials for each novel word was 150, presented across ~30 minutes. In STUDY IV, the significant response increase exhibited by the control children occurred once the word-form was repeated 135-270 times within only 6 minutes. In previous studies, the novel word-forms were repeated 160 times within different time ranges (Shtyrov et al., 2010b; Shtyrov, 2011; Yue et al., 2014). The number of repetitions required to induce the response enhancement in STUDIES II and IV with two different age groups overlaps, emphasising the importance of sufficient number of repetitions in this effortless, automatic, form of word memory-trace development. It should be further investigated whether increasing the number of novel items, with the coincident increase in exposure time, has any effects on the neural dynamics. With respect to this, and more importantly, by adding the number of different tokens, the number of repetitions per novel item could be varied and adequate signal-to-noise of the ERP secured. Such comparisons would enable further testing whether 150 repetitions is the ‘magic number’ critical in establishing rapid neural word learning.

Furthermore, the proposition that the activation of lexical competitors (i.e. known words that are phonologically matched with the novel words) during the learning process is critical for perceptual learning to engender lexicalisation effects without consolidative sleep (as suggested by Lindsay & Gaskell, 2013) should be verified.

Relatedly, Szmalec et al. (2012) reported such lexicalisation effects without sleep with a sequence learning paradigm that did not incorporate existing lexical items during exposure to the visually presented sequences, mimicking studies of language learning from speech streams (e.g. Saffran et al., 1996; De Diego Balaguer et al., 2007; Cunillera et al., 2009). Furthermore, in this study, lexicalisation effects were tested with auditorily presented sequences, suggesting that fast learning through Hebbian principles may result in word representations that can be accessed cross-modally.

In EEG, the reflection of the underlying neural activity distributions is manifested by scattered scalp topography. Thus, the topography does not directly reveal the locations of the electrical current sources generating the ERPs. In order to resolve this inverse problem, source modelling methods are used. Given the lack of individual MRIs, the source modelling in the studies of this thesis was conducted with either standard age-appropriate head models (STUDIES I and IV) or an ellipsoidal head model (STUDY II). Consequently, strict correspondence with electrode positions and individual cortex was not obtained. Thus, the accuracy in small scale structural distinctions (such as the different parts of the IFG) of the reported distributed source locations should be considered with caution. Nevertheless, generally the source results were supported by literature and in STUDY II the sources were estimated according to literature-driven a priori defined locations.

## **5.5 LIMITATIONS AND FUTURE DIRECTIONS**

The STUDIES have some limitations worth discussion. A clear drawback in the experimental paradigm of STUDY IV was that no known word was presented as in STUDY II. Thus, STUDY IV could not indisputably confirm whether the response increase in the normal-reading children is established solely to novel word-forms and not to known ones, as is shown in adults. Furthermore, the possibility that other, non-linguistic, auditory processing mechanisms might account for the observed neural learning effect of the speech stimulus in the control children, and the lack thereof in the dyslexics, cannot be completely ruled out. Consequently, future studies should include known words as well as a larger set of novel words in order to validate the specificity of the direction of the response change and, on the other hand, define whether the effect observed in children in STUDY IV is language-specific by

administrating acoustic-phonetically carefully matched lexical and non-lexical items to see if the neural dynamics differentiate between lexical categories and non-verbal sounds. Relatedly, it should be investigated whether the neural repetition *suppression* mechanism in general works similarly in dyslexic and control individuals, e.g. by employing non-linguistic familiar stimuli. Such experiments could give insight into the debate on whether dyslexia is related to a low-level auditory processing deficit (Banai & Ahissar, 2006; Goswami, 2015).

In general terms, the investigation of the neural bases for rapid learning of new words under perceptual exposure should be extended to different modalities (i.e. written words) and language domains (i.e. word production). Also, while repetition of signal-correlated noise was found not to elicit response enhancement (Shtyrov, 2011), the exposure-related learning phenomenon should be further defined using more variable novel non-linguistic stimuli such as ‘musical rain’, which shares acoustic properties of speech but is not perceived as speech (Uppenkamp et al., 2006).

Furthermore, the role of the initial rapidness of learning words in the successful integration to the mental lexicon and long-term retention should be elaborated, e.g. by determining the effect of sleep and passage of time in the consolidation, as discussed in Section 5.1. While behavioural tasks may index lexicalisation in indirect means, reliable neural markers of lexicalisation are currently non-existent. At the same time, the possible (micro)structural plastic changes related to the functional rapid memory-trace formation for new words are yet to be discovered. To get a comprehensive neurobiological view on the rapid word learning phenomenon, the possible role of subcortical structures, especially the hippocampus, requires future investigation.

And finally, the findings of STUDY III should be taken into consideration in studies of language learning, since non-native learning in later childhood and adolescence seems to have a compelling association with novel non-native and native word learning. Relatedly, ‘monolingual’ speakers might in fact have learnt and use non-native languages without considering themselves as bi- or multilinguals, prompting inquiry.

## 6 CONCLUSIONS

The studies of the current thesis manifested a robust effect of increasing exposure in neural responses to words. Namely, stronger amplitude of an early response, locked to the lexical disambiguation point of the spoken word, was established for word-forms with more past exposure compared to those that subjects were less frequently exposed to, or that were completely novel. The enhanced amplitude is suggested to indicate stronger word memory traces, i.e. cell assemblies or networks, in the brain. This was concluded from short-term experimentally induced exposure lasting for tens of minutes, as well as with long-term exposure consisting of the entire past life. Increasing exposure was associated with increasing amplitude; however, the studies did not examine the permanence of the achieved amplitude between the short and very long periods of time. The effect was found for ignored spoken input in both short- and long-term exposure, which refers to automatic and effortless activation and formation of word memory traces. The reliability of the interpretation of the neural exposure effect as an index of memory-trace strength was verified by significant associations found for multiple sources of information and measures on collective and individual memory.

The efficiency of such rapid neural learning for novel native words outperformed that of novel non-native words. This was inferred from less robust response increase to words with unfamiliar phonology that did not reach significance in the time the response to novel native words did. The individual variability in the magnitude of response change was significantly associated with how many foreign languages one had learnt and at which age the learning had commenced on average. Furthermore, the average age of acquisition of the non-native languages was associated with the extent of response change within short-term exposure to novel native words as well. These results suggest that the underlying language network, which has developed through personal experience with the native and possible further languages, is in contact with the rapid word learning process. Furthermore, the interaction of how the brain responds to novel sensory input over time with the pre-existing language network seems to be general to any type of novel phonological material.

Critically, the paradigms and stimuli used in the studies enabled the scrutiny of the phonological-lexical in opposition to the lexico-semantic word-form. Thus, it is possible to conclude that semantic associations are not imperative for robust lexical learning. This inference inclines to emphasise speech as a unique type of sensory input to humans without the necessary requirement for a definite affiliation with meaning. This notion also corroborates the extraordinary capacity of the brain to process and store spoken input.

The rapid increase in response amplitude during brief exposure was observed in healthy adults and school-aged children. However, this phenomenon was not found in children with dyslexia. Dyslexics showed a remarkably distinct pattern of neural dynamics during brief exposure to novel words, implying impairment in the initial encoding of new phonological word-forms as the underlying reason for the widely reported difficulty in learning new words in dyslexia.

Source reconstructions for the enhanced responses, whether due to brief or long-lasting exposure, showed noticeable left-lateralisation for words with higher occurrence as well as for the process of recurrence. The left perisylvian cortex, especially the inferior frontal and temporal regions, was the origin for the enhancement in adults. Memory-trace formation involved posterior temporal areas, whereas the memory-trace activation of words with extensive long-term exposure originated from more anterior temporal cortex. In children, on the other hand, bilateral prefrontal cortex underpinned the activation increase during brief exposure to novel words, with slight lateralisation to the left hemisphere. This gives some indication of maturational differences in the brain areas responsible for the neural word learning process between the developing and the more mature cortex. In sum, the results of this thesis are in line with the neurobiological theory of language endorsing Hebbian neural learning as the mechanism for the formation and activation of word memory circuits.

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