

COGNITIVE NEUROSCIENCE

Native vs. second language discrimination in the modulation of the N400/N400m

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Abstract

The N400 evoked response component, initially proposed as a marker of semantic incongruity, was later demonstrated to be evoked by various potentially meaningful stimuli, such as words or pseudowords. The present study tested whether the N400 elicited by isolated words and pseudowords was modulated by task instructions thus reflecting controlled processing of linguistic information. In two language discrimination tasks, Finnish adults with English as their second language detected either Finnish or English nouns in a list of Finnish and English words and pseudowords. The same set of stimuli, presented in a random order, was used for both tasks. The amplitudes of both the evoked potentials and their magnetic counterparts were task-language dependent. In both tasks, task-language pseudowords elicited more negative evoked potentials (N400 and P600) than non-task-language pseudowords or words. The left temporal source of the evoked magnetic field was activated more strongly by English than Finnish pseudowords in the English task. This source was also activated more strongly by English pseudowords in the English task than in the Finnish task. However, no similar enhancement of the evoked magnetic field by Finnish pseudowords was observed in the Finnish task. This finding suggests that at the level of multimodal temporal cortex around the superior temporal sulcus, the native language is processed more automatically than the second language and that the controlled processing of linguistic information reflected by the N400 potential is accomplished by a broader neural network extending beyond the association temporal areas.

Introduction

The N400 component of evoked responses was initially proposed as a marker of semantic incongruity (Kutas & Hillyard, 1980). When compared with responses elicited by expected sentence endings, inappropriate words occurring at the end of a sentence evoked a negative potential in central and parietal electrodes peaking at around 400 ms. It was later demonstrated that the N400 can be elicited without sentence context, by word lists or even by pseudowords, and it can be influenced by various psycholinguistic factors (Rugg, 1984; Bentin *et al.*, 1985; Besson & Kutas, 1993; Kutas & Van Petten, 1994; Debrulle, 1998; Radeau *et al.*, 1998; Kutas & Federmeier, 2011; Laszlo *et al.*, 2012; Dickson & Federmeier, 2014). The influence may be directly related to the nature of the stimulus words. For example, the N400 to rare words is stronger than the N400 to high-frequency words (Smith & Halgren, 1987; Van Petten & Kutas, 1990). More interestingly, the context where the word occurs can also influence the magnitude of the N400. For example, repetition, semantic, and phonological priming reduce the

N400 effect (Kutas & Van Petten, 1994; Kutas & Federmeier, 2011). In addition, language proficiency and dominance affect the N400 in bilinguals (Kutas *et al.*, 2009). Overall, the N400 is thought to reflect stimulus-induced semantic activity (Kutas & Federmeier, 2011). However, the details of the underlying processes are far from clear.

Multiple linguistic and non-linguistic studies have shown that physically identical stimuli elicit distinct neural responses depending on the context in which the stimuli are presented. For example, brain responses to identical sounds or visual images vary depending on the type of cognitive task, such as processing of spatial vs. non-spatial features (Anurova *et al.*, 2005; Vuontela *et al.*, 2009), discrimination of vowels vs. speakers' voices (Bonte *et al.*, 2009, 2014) or using native vs. second language for naming numbers (Blanco-Elorrieta & Pylkkanen, 2015). The strong effect of context on the N400 implies that the same word evokes an N400 of varying amplitude depending e.g., on the preceding sentence or the prime word (Lensink *et al.*, 2014). Furthermore, the level of processing may also affect the N400. An N400 priming effect observed in a lexical decision task disappeared during discrimination of physical properties of the presented words (Chwilla *et al.*, 1995). Similarly,

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concrete words elicit stronger N400 than abstract words in tasks requiring postlexical semantic processing, but not during simple letter search (West & Holcomb, 2000). Modulations of the N400 may be also observed at a prelexical level of processing. Such modulations are known as the orthographic neighborhood size effect (Holcomb *et al.*, 2002) and the first syllable frequency effect (Barber *et al.*, 2004; Hutzler *et al.*, 2004; Bles *et al.*, 2007). A word with a large orthographic neighborhood, defined as the group of words that are of the same length as the target, but differ from it by only one letter, elicits a larger N400 than a similar word with a small neighborhood. Consistently with a Cohort model of lexical retrieval (Marslen-Wilson, 1987), these results suggest that a word with a large neighborhood, in addition to the representation of the word itself, also activates representations of other words in its neighborhood. In groups of bilinguals the neighborhood size effect may even be observed across languages (Midgley *et al.*, 2008). Similarly, a word with a high-frequency first syllable elicits more prominent N400 compared to a word with a low-frequency first syllable due to activation of a larger cohort of possible lexical candidates (Barber *et al.*, 2004; Hutzler *et al.*, 2004).

The N400 is often followed by the Late Positive Component (the P600) which is traditionally associated with responses to syntactic violations (Kuperberg, 2007). The P600 is present when syntactic violations are embedded not only in real sentences, but also in meaningless Jabberwocky sentences that are semantically impoverished, but retain the syntactic structure (Yamada & Neville, 2007; Hahne & Jescheniak, 2001). In Jabberwocky sentences, all function words that express grammatical relationships within a sentence are preserved, while content words are replaced with pseudowords. The latter finding indicates that syntactic processes are at least relatively independent from the presence of lexical-semantic information (Hahne & Jescheniak, 2001). However, a slight yet significant attenuation of the P600 response to meaningless compared to regular sentences suggests that semantic and syntactic information processing is not dissociated but rather integrated in neural networks (Yamada & Neville, 2007).

In responses to sentences including combined semantic and syntactic violations, both the N400 and the P600 effects were present (Gunter *et al.*, 2000; Hagoort, 2003; Martin-Loeches *et al.*, 2006). Therefore, during on-line language comprehension, the N400 and P600 may represent two consecutive stages of language processing. The evaluation of the semantic and syntactic properties of each upcoming word takes place during the N400 time window. This evaluation relies on lexical search and retrieval from long-term memory and results in fitting the word into the preceding semantic context. If the word cannot be integrated semantically into the preceding context, the N400 is elicited. The P600 may reflect syntactic integration difficulty, since its amplitude correlates with various types of syntactic violations and with processing of syntactically complex sentences, which may require revision (Kaan *et al.*, 2000; Friederici, 2002; Friederici & Weissenborn, 2007). In other words, the P600 may be linked to construction or updating of a mental representation of the communication content (Brouwer *et al.*, 2012). However, despite strong association of the P600 with high-level linguistic processes, it has been shown to share features with the P3b. As the P3b, the P600 is sensitive to stimulus probability (Gunter *et al.*, 1997; Coulson *et al.*, 1998), and its latency correlates strongly with reaction times (RTs) (Sassenhagen *et al.*, 2014; Sassenhagen & Bornkessel-Schlesewsky, 2015). Furthermore, the P600 may be present in responses to word lists and to pseudowords (Kanske & Kotz, 2007; Bermudez-Margaretto *et al.*, 2015). Thus, when neither semantic nor syntactic context is present, the late

positivity may index general cognitive processes serving, for example, as a marker of stimulus probability and cognitive demands.

It has been debated whether modulations of the N400 amplitude reflect automatic processes, controlled processes or both. In line with the aforementioned Cohort model, the orthographic neighborhood and the first syllable frequency effects, which are associated with lexical search and lexical access, are highly automatic in both spoken and written language comprehension (Holcomb *et al.*, 2002; Barber *et al.*, 2004; Hutzler *et al.*, 2004; Midgley *et al.*, 2008). Priming studies using highly degraded or masked stimuli (Deacon *et al.*, 2000; Wang & Yuan, 2008), show a modulation of the N400 regardless of a subject's awareness of word identity suggesting that the N400 indexes exclusively automatic processes. However, successful performance of the lexical decision task may require the involvement of additional cognitive processes controlled by higher-order cognitive functions such as selective attention. In the visual modality, priming effects at short intervals between prime and target words are considered to result from rapid but short-acting automatic spreading of activation from the corresponding conceptual representation of the prime stimulus to related words in semantic memory (Collins & Loftus, 1975). With longer intervals there is enough time to integrate prime and target words into a semantic context. Consequently, it has been suggested that, in experiments with a lexical decision task, the automatic process of lexical access is followed by a controlled process of semantic integration (Silva-Pereyra *et al.*, 1999; Hill *et al.*, 2002).

The present study was designed to maximize the possible effects of controlled processing while minimizing the effects of priming. For this purpose the same sets of stimuli (Finnish and English words and pseudowords, meaningless letter strings that obey Finnish or English orthographic rules) were presented in a random order in two experimental tasks, the Finnish and English language tasks. Furthermore, semantic processing was not required for successful task performance. Depending on task instructions, subjects had to detect either Finnish or English nouns. Subjects were late bilinguals with Finnish as their first and English as their second language. We aimed to test whether both electric and magnetic counterparts of the N400 elicited by visually presented words and pseudowords are modulated by task instructions and thus reflect controlled processing of linguistic information. If the same group of stimuli (e.g., English-language pseudowords), which jointly provide the same number of orthographic neighbors and first syllable/word frequencies, were to elicit N400 responses of different amplitudes depending on the context (task language), it would suggest involvement of additional mechanisms of cognitive control. The involvement of such mechanisms may be more evident for foreign language processing as requiring more demanding lexical search and retrieval. Taking into account that the N400 may be enhanced by semantic or conceptual processing difficulty (Monetta *et al.*, 2003; Hubbard *et al.*, 2014), we also hypothesized that the most difficult experimental conditions in each task (i.e., discriminating between task-language words and task-language pseudowords) would induce the most prominent N400 effect.

A considerable body of electrophysiological (Helenius *et al.*, 1998; Halgren *et al.*, 2002; Lau *et al.*, 2008; Uusvuori *et al.*, 2008; Blanco-Elorrieta & Pylkkanen, 2015) and neuroimaging studies (Baumgaertner *et al.*, 2002; Copland *et al.*, 2003; Kuperberg *et al.*, 2003; Rissman *et al.*, 2003; Matsumoto *et al.*, 2005; Van Petten & Luka, 2006) converge on the principal role of the left temporal lobe (superior/middle temporal gyri) in the generation of the N400 effect, with lesser contribution of the right temporal lobe. Moreover, transcranial magnetic stimulation of the left temporal lobe was shown to

selectively disrupt semantic task (synonym judgment) but not control task (number judgment) performance when the pulses were delivered at a time point of 400 ms from the stimulus onset (Jackson *et al.*, 2015). Thus, we expect that task-related modulations of the N400 will be observed mainly (or exclusively) in the left hemisphere.

Materials and methods

Subjects

The subjects were 10 healthy right-handed Finns (mean age 25 years, range 22–30 years, six females) with monolingual Finnish family backgrounds. All subjects had a high level of English proficiency, having studied English for 7–9 years, beginning at 9–11 years of age. The subjects received either ‘good’ or ‘excellent’ grades on their high school English language matriculation exam. All subjects had normal or corrected to normal vision. All participants gave their informed consent before the experimental session. The study protocol was approved by the Ethics Committee of the Helsinki and Uusimaa Hospital District.

Experimental stimuli

Stimuli were visually presented four-to-six-letter strings, which comprised 160 Finnish words, 160 English words and 160 pseudowords (80 Finnish and 80 English pseudowords). Finnish words were chosen among the 4000 most frequent words (Saukkonen *et al.*, 1979), and English words among 3000 most frequent words used in teaching English in the Finnish school system (Ahti, 1984). The stimuli were presented randomly in two blocks, both blocks consisting of the same 480 stimuli with different task instructions. The stimuli were written in white lower case letters that appeared on a dark gray background for 300 ms with a 750 ms interstimulus interval. The stimuli were projected onto a screen located 1.7 m from the subject inside a magnetically shielded room. The delivery of the stimuli was controlled by a computer program (Presentation 0.31; Neurobehavioral Systems, Inc., San Francisco, CA, USA). This program was also used for collecting the behavioral data (correct/incorrect responses and RTs).

Behavioral tasks and analysis

Subjects performed two different language discrimination tasks (English and Finnish) (Fig. 1). In both tasks the subjects were required to respond to each visual stimulus by pressing either a YES- or NO-button according to task instructions. In the English task, subjects pressed the YES-button with the left index finger if the stimulus was an English word (a task-language word) and the NO-button with the left middle finger in response to all other types of stimuli: Finnish words (non-task-language words) and either English or Finnish pseudowords (task-language pseudowords or

non-task-language pseudowords respectively). In the Finnish task, the YES-response corresponded to Finnish words and the NO-response to other stimuli. The stimulus type will be also referred to as an experimental condition in the text. Each task was presented once during the experimental session, and the order of the tasks was balanced across subjects. Before the real experiment started, the subjects had a short practice session with a set of stimuli not belonging to the experimental stimulus set.

Statistical analysis of the RTs was performed using a two-way ANOVA with the factors of task language (English or Finnish) and stimulus type (task-language pseudowords, non-task-language pseudowords, task-language words, or non-task-language words). If significant main effects or interaction of the effects were observed ($P < 0.05$), *post hoc* analyses were performed using the Newman–Keuls test. The Greenhouse–Geisser correction was used for factors with more than two levels. Error rates (where errors included both incorrect responses and omissions) were analyzed by planned comparisons using Wilcoxon signed rank test. The P -values were adjusted using the Bonferroni correction (by multiplying each uncorrected P -value by the number of comparisons). The corrected P -values < 0.05 were considered statistically significant.

Neurophysiological data collection and analysis

Neurophysiological data were recorded in the BioMag laboratory of Helsinki University Central Hospital using simultaneous whole-head MEG (306-channel Elekta Neuromag[®] magnetometer; Elekta Neuro-mag Ltd, Helsinki, Finland) and EEG (64-channel Ag/AgCl-electrode cap). The data were recorded in a magnetically shielded room (Euroshield, Eura, Finland). The reference electrode was placed on the nose and the ground electrode on the left cheek. In addition, vertical and horizontal electro-oculograms (EOG) were recorded. The analog recording passband was 0.03–100 Hz and the sampling rate 600 Hz. Epochs starting 100 ms before and ending 900 ms after the stimulus onset were averaged online. Epochs containing artifacts (EOG or EEG variation $\geq 150 \mu\text{V}$, MEG variation $\geq 1500 \text{ fT/cm}$) or incorrect responses were automatically excluded from the analysis. Signal amplitudes were defined with respect to the baseline, which was determined as the average signal amplitude during the 100-ms period preceding stimulus onset.

The event related potentials (ERPs) were analyzed within a set of 6 electrodes (Fig. 3A), where the N400 was most prominent. The ERPs were digitally filtered with a passband of 0.5–20 Hz. The amplitudes of the N400 were determined as the mean amplitudes over two consecutive 200-ms time windows: 300–500 ms, a traditional N400 window, and 500–700 ms from the stimulus onset, which usually corresponds to a slow positive deflection (P600) following the N400. The later time window enables detection of possible P600 effects and/or the N400 effects when the N400 is lengthened in duration. However, response-related activity reflected by slow positive components of evoked responses, such as P3b and the following Positive Slow Wave (PSW), also takes place during

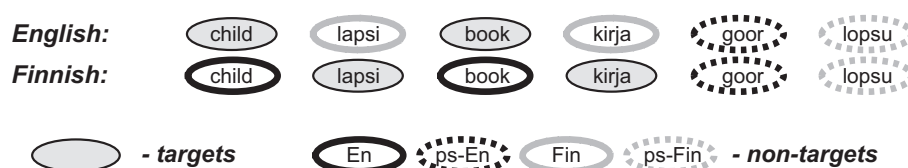


FIG. 1. Schematic representation of the behavioral tasks and examples of the stimuli. En, English words; Fin, Finnish words; ps-En, English pseudowords; ps-Fin, Finnish pseudowords.

the analyzed time intervals. It has been shown that the P3b and PSW differ significantly between positive and negative probes, with the P3b being larger for positive than negative probes, and the PSW, conversely, larger for negative ones (Pelosi *et al.*, 1998; Anurova *et al.*, 2005). Therefore, in order to exclude the possible effect of the response type (YES to targets vs. NO to non-targets), only epochs corresponding to non-target stimuli were analyzed in the present study.

The amplitude values were collected for each subject from each electrode site of the 6-electrode set. For statistical comparison of the N400 amplitudes, a four-way ANOVA was applied. The factors were time interval (300–500 or 500–700 ms), task language (English or Finnish), stimulus type (task-language pseudowords, non-task-language pseudowords, or non-task-language words) and electrode (six sites). The Greenhouse-Geisser correction was used for factors with more than two levels. *Post hoc* analyses were performed using the Newman–Keuls test.

Source configurations underlying the MEG data sets were modeled using the minimum current estimate (MCE) algorithm (Elekta Neuromag Ltd.; Uutela *et al.*, 1999). Both planar gradiometers (102 pairs) and magnetometers (102) were used for MCE calculation. MCEs were calculated separately for each individual subject and for all six experimental conditions (three stimulus types in both tasks). Averaged evoked responses were first filtered using the Xplotter from the Neuromag toolbox with a passband of 0.5–20 Hz and saved with fixed filter settings. Next, the epochs were processed using the MCE. The baseline correction was done for the 100-ms period preceding stimulus onset. Computations were performed for each time sample of the entire epoch starting from 100 ms before and up to 900 ms after the stimulus onset using the spherically symmetric conductor model. The head coordinate system was defined for each subject by locating the preauricular points and nasion (cardinal points) with a three-dimensional digitizer Isotrak (Polhemus Inc., Colchester, VT, USA). The locations of the four position-indicator coils, attached to the subjects' head, were determined with the digitizer with respect to the three cardinal points. The head position within the magnetometer helmet was determined by letting current pass through the indicator coils and by recording the induced magnetic signals. Head position information was recorded at the beginning of each block and used in the source modeling procedure. The differences between the head position measurements for each block did not exceed 2.5 mm along the *x*-axis, 4 mm along the *y*-axis and 5.1 mm along the *z*-axis. The origin of the spherical model was set at $x = 0$, $y = 0$ and $z = 50$ mm.

Source current distributions were compared across subjects and experimental conditions. Visual inspection revealed several cortical areas which were active at the time interval corresponding to the N400 response: temporal, occipital, parietal, and prefrontal. Only the temporal generators of the N400m, consistently found in all subjects and experimental conditions, were considered for further analysis. Regions of interest (ROI) were determined individually for each subject and condition as brain volumes with the largest current amplitudes within the temporal areas. The extent of each ROI and its center coordinates were automatically adjusted to fit the estimated activity. The time courses of the activity within the selected areas were calculated as a spatially weighted average of the estimate with the maximal weight (1.0 in the sum) at the center of the volume. The weight extended to the neighboring locations with the form of a three-dimensional generalized normal distribution, and the weight of the border points corresponded to 60% of the weight of the center. The same 200-ms integration windows (300–500 and 500–700 ms) were used for the analysis of the source activity. For the statistical

analysis of the source amplitudes, a four-way ANOVA was used with the factors of time interval (300–500 or 500–700 ms), task language (English or Finnish), stimulus type (task-language pseudowords, non-task-language pseudowords or non-task-language words) and hemisphere (left or right). Analysis of the source locations was performed at the 300–500 ms time interval, which corresponded to the source activity maxima. A three-way ANOVA with the same factors, except the factor of time interval, was used. The Greenhouse-Geisser correction was used for factors with more than two levels.

Planned comparisons were performed using the Least Significant Difference test. Source activities were compared across the experimental conditions in each hemisphere and each time interval. In addition, responses to the same type of pseudowords were compared between English and Finnish tasks. The *P*-values were corrected for multiple comparisons using the Bonferroni correction.

Results

Behavioral data

Analysis of the task performance accuracy revealed that during performance of the English task, subjects made more errors responding to English pseudowords than to Finnish pseudowords ($Z = 2.8$, $P = 0.020$). During performance of the Finnish task, the subjects made more errors responding to Finnish pseudowords compared to English pseudowords ($Z = 2.7$, $P = 0.031$) (Fig. 2A). Furthermore, both types of pseudowords were processed differently during the performance of the English and the Finnish tasks: subjects made more mistakes responding to English pseudowords presented during the English task than the Finnish task ($Z = 2.8$, $P = 0.020$) and vice versa, to Finnish pseudowords presented during the Finnish task than the English task ($Z = 2.5$, $P = 0.047$).

The RTs were affected by the task language ($F_{1,9} = 6.1$, $P = 0.036$, $\eta_p^2 = 0.40$, Power = 0.60) and stimulus type ($F_{3,9} = 44.2$, $P = 3.8 \times 10^{-7}$, $\eta_p^2 = 0.86$, Power = 1.00), and there was a significant task language and stimulus type interaction ($F_{3,27} = 27.3$, $P = 4.2 \times 10^{-5}$, $\eta_p^2 = 0.75$, Power = 1.00). The RTs were longer during the English than the Finnish task. Furthermore, the longest RTs were observed for the task-language pseudowords compared to non-task-language pseudowords ($P = 1.7 \times 10^{-4}$), non-task-language words ($P = 1.3 \times 10^{-5}$), or target words ($P = 1.4 \times 10^{-5}$). This result was also true for each language task separately ($P = 1.7 \times 10^{-4}$, $P = 1.3 \times 10^{-4}$, $P = 1.3 \times 10^{-4}$ for the English task, and $P = 1.4 \times 10^{-4}$, $P = 0.001$, $P = 5.1 \times 10^{-4}$ for the Finnish task) (Fig. 2B). In addition, in the Finnish task responses to non-task-language pseudowords were faster than responses to non-target ($P = 0.002$) or target words ($P = 0.003$). Furthermore, responses to the same type of pseudowords were always faster when the pseudowords were used as non-task-language than as task-language ($P = 1.4 \times 10^{-4}$ and $P = 0.005$ for English and Finnish pseudowords respectively).

EEG data

Analysis of the visual evoked potentials (Fig. 3B) was performed in two consecutive 200-ms time windows (300–500 and 500–700 ms) within the 6-electrode matrix (Fig. 3A). For the language tasks, the four-way ANOVA showed that the amplitudes of the evoked potentials were affected by the main factors of time interval ($F_{1,9} = 27.4$, $P = 5.4 \times 10^{-4}$, $\eta_p^2 = 0.75$, Power = 1.00) and stimulus type ($F_{2,18} = 5.3$, $P = 0.031$, $\eta_p^2 = 0.37$, Power = 0.77), and there was a significant time interval, task language, and stimulus type interaction

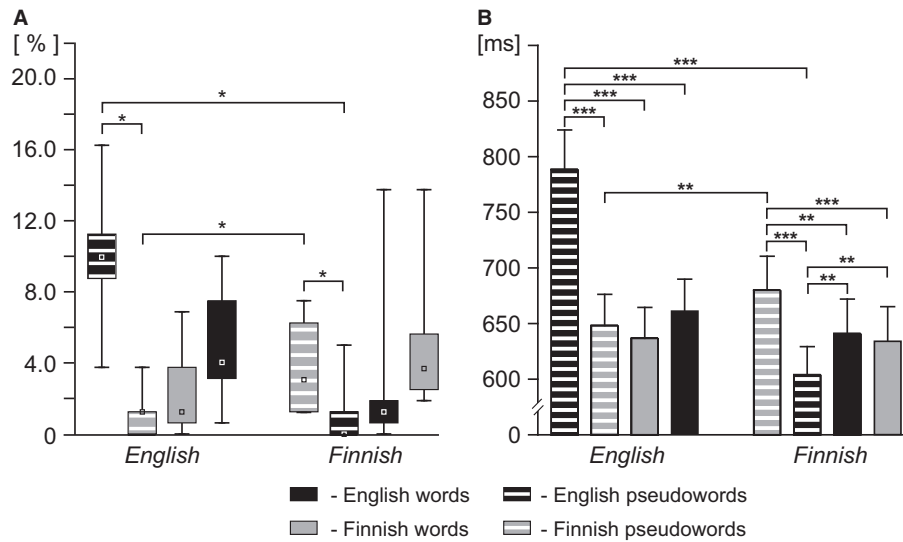


FIG. 2. Behavioral data. (A) Box-and-whisker plot illustrating error rates during performance of the English and Finnish language tasks. Boxes represent the interquartile range, with the small square inside the box corresponding to the median, and whiskers extending from minimum to maximum values. (B) Mean reaction times \pm standard error of the mean (vertical lines). The rightmost box/bar in each task corresponds to the responses to target words (English in the English task and Finnish in the Finnish task). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

($F_{2,18} = 5.6$, $P = 0.016$, $\eta_p^2 = 0.38$, Power = 0.79). The mean ERP amplitudes were more negative within the first time window than in the second time window. They were also generally more negative in the responses to the task-language pseudowords than to the non-task-language pseudowords ($P = 0.013$) or real words ($P = 0.026$). Furthermore, in the Finnish task this effect was observed during the first time interval ($P = 0.039$ and $P = 0.029$ respectively), while in the English task during the second time interval ($P = 9.1 \times 10^{-4}$ and $P = 8.2 \times 10^{-4}$ respectively) (Fig. 3B and D). When responses to the same type of pseudowords were compared between the two tasks using planned comparisons, a significant difference was found for English but not Finnish pseudowords. English pseudowords elicited more negative responses during the English than the Finnish task performance within the second time window ($P = 0.002$; Fig. 3C and D). No other significant effects or interactions were observed.

MEG data

All stimulus types in both tasks elicited clear evoked fields at the time intervals corresponding to the N400 and the following P600 over association temporal cortex within the superior temporal gyrus and sulcus. The activity was more pronounced over the left hemisphere (Fig. 4).

Using MCE allowed the modeling of temporal sources of the magnetic counterpart of the N400 in both hemispheres. Figure 5 shows grand average MCEs for the N400 elicited by different stimuli in the two language tasks.

Statistical analysis of source activity revealed that in both tasks, amplitudes of the temporal generators of the N400 were affected by the time interval ($F_{1,9} = 12.98$, $P = 0.006$, $\eta_p^2 = 0.59$, Power = 0.89) and stimulus type ($F_{2,18} = 6.18$, $P = 0.020$, $\eta_p^2 = 0.41$, Power = 0.83). The most prominent temporal activity was elicited by the task-language pseudowords, while the lowest activity was elicited by real non-target words. The amplitudes of the temporal generators of the N400 in the responses to the task-language pseudowords were larger than in the responses to the

non-task-language pseudowords ($P = 0.041$) or words ($P = 0.007$). Furthermore, there was a significant hemisphere and stimulus type interaction ($F_{2,18} = 4.66$, $P = 0.048$, $\eta_p^2 = 0.34$, Power = 0.71). In the left hemisphere activity differed significantly among all three stimulus types: task-language pseudowords vs. non-task-language pseudowords ($P = 0.037$) or words ($P = 4.7 \times 10^{-4}$), and non-task-language pseudowords vs. words ($P = 0.018$). In the right hemisphere, in contrast, no significant differences were observed. Interhemispheric differences in source activity (left > right) were significant for both types of pseudowords (task-language, $P = 5.0 \times 10^{-4}$ and non-task-language, $P = 0.004$) but not real words ($P = 0.56$). Finally, there was a significant time interval, hemisphere and stimulus type interaction ($F_{2,18} = 4.32$, $P = 0.037$, $\eta_p^2 = 0.32$, Power = 0.67). During the earlier time interval both types of pseudowords elicited stronger responses in the left hemisphere than real words (task-language pseudowords vs. non-target words, $P = 1.5 \times 10^{-4}$ and non-task-language pseudowords vs. non-target words, $P = 1.9 \times 10^{-4}$). During the later time interval, however, left-hemispheric responses to task-language pseudowords were significantly stronger than responses to non-task-language pseudowords ($P = 0.027$) or words ($P = 0.014$). No significant differences were found in the right hemisphere. Interhemispheric differences in source activity were confined to the responses to pseudowords (task-language, $P = 1.4 \times 10^{-4}$ and non-task-language, $P = 1.6 \times 10^{-4}$) elicited during the earlier time interval.

Planned comparisons revealed that significant differences in source activity between the experimental conditions were observed exclusively in the left hemisphere (Fig. 6). During the 300–500 ms time interval the left temporal generator of the N400 was activated more strongly by both types of pseudowords compared to real words (English task, English and Finnish pseudowords vs. Finnish words: $P = 2.5 \times 10^{-5}$ and $P = 2.0 \times 10^{-4}$ respectively; Finnish task, Finnish and English pseudowords vs. English words: $P = 9.7 \times 10^{-4}$ and $P = 0.034$ respectively). Moreover, English pseudowords elicited stronger responses during the English task than during the Finnish task ($P = 0.014$). This difference remained significant throughout the later time interval ($P = 0.010$). No significant

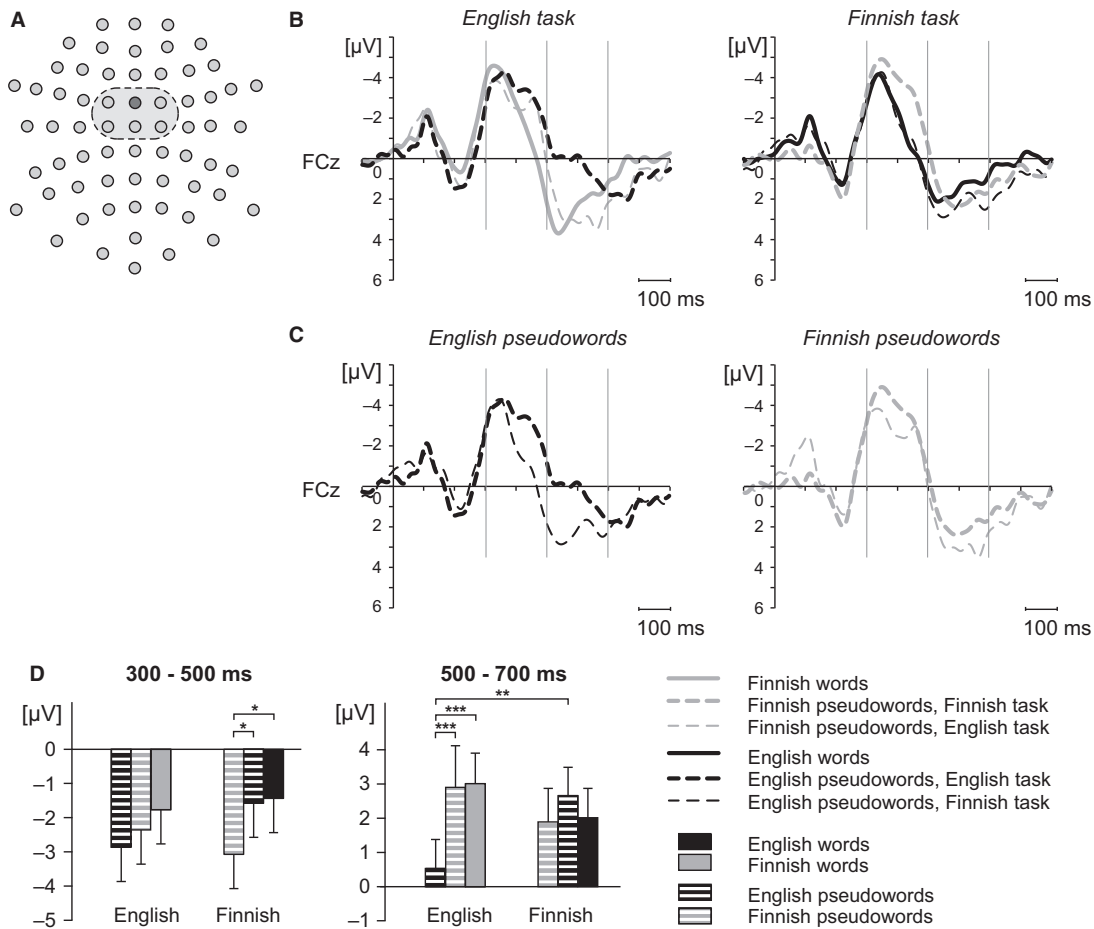


FIG. 3. (A) The 6-electrode set for the analysis of the amplitudes of the evoked potentials. The fronto-central (FCz) site is marked in dark gray. (B) Grand average visual evoked potentials to non-target stimuli recorded at the FCz site during the English and Finnish tasks (negative up). (C) Superimposition of the responses to the same types of pseudowords recorded during the two tasks. Light vertical lines show the 300–500 and 500–700-ms time intervals. (D). Group mean amplitude of the evoked potentials \pm standard error of the mean (SEM) averaged across the 6-electrode set during the 300–500 and 500–700-ms time intervals. The vertical lines indicate SEM, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

modulations of source activity were found for the Finnish task at 500–700 ms. However, during the English task, English pseudowords activated the left temporal source more strongly than Finnish pseudowords ($P = 0.004$) or Finnish words ($P = 0.004$) at the later time interval.

Statistical evaluation of the source coordinates indicated that neuronal generators of the N400 elicited in both language tasks were located within the superior temporal gyrus/superior temporal sulcus (Fig. 7). Furthermore, source locations were similar across language tasks and experimental conditions.

Discussion

The present study was designed to test whether the N400 elicited by real and pseudowords in two language discrimination tasks is modulated by task instructions, and thus whether it reflects controlled processing of linguistic information. Simultaneous EEG/MEG measurements were performed in order to compare the EEG responses evoked by broad underlying areas and MEG responses evoked by more localized areas in the temporal lobes. We found that the same stimuli presented during different experimental tasks elicited N400 potentials of different magnitudes. Task-language pseudowords elicited more negative evoked potentials than either

non-task-language pseudowords or words due to enhancement of the N400. This effect was observed within the 300–500 ms time interval during the Finnish task and was delayed until the 500–700 ms time interval during the English task. Furthermore, within the later time interval, the same English pseudowords elicited more negative responses during the performance of the English task than the Finnish task, indicating differences in the timing of the task performances and suggesting that the N400 evoked potential reflects controlled processing of linguistic information. It is worth emphasizing that the amplitude difference in evoked potentials between the two types of pseudowords was observed earlier in the Finnish task than in the English task. This finding is in line with earlier observations of longer latencies of the N400 that is elicited by sentence-ending incongruous words (Moreno & Kutas, 2005) or word lists (Midgley *et al.*, 2009) presented in a non-dominant language. It is also in line with the later onset of the N400 that is elicited in non-native compared to native speakers by a reversed word order in noun-noun compounds (De Cat *et al.*, 2015). Our results thus support the notion that second-language processing is slower.

An important question that arises is whether modulations of the evoked responses observed during the later time interval reflect the delayed/prolonged N400 effects or modulations of the overlapping P600. Since in the present study the stimuli were lists of words and

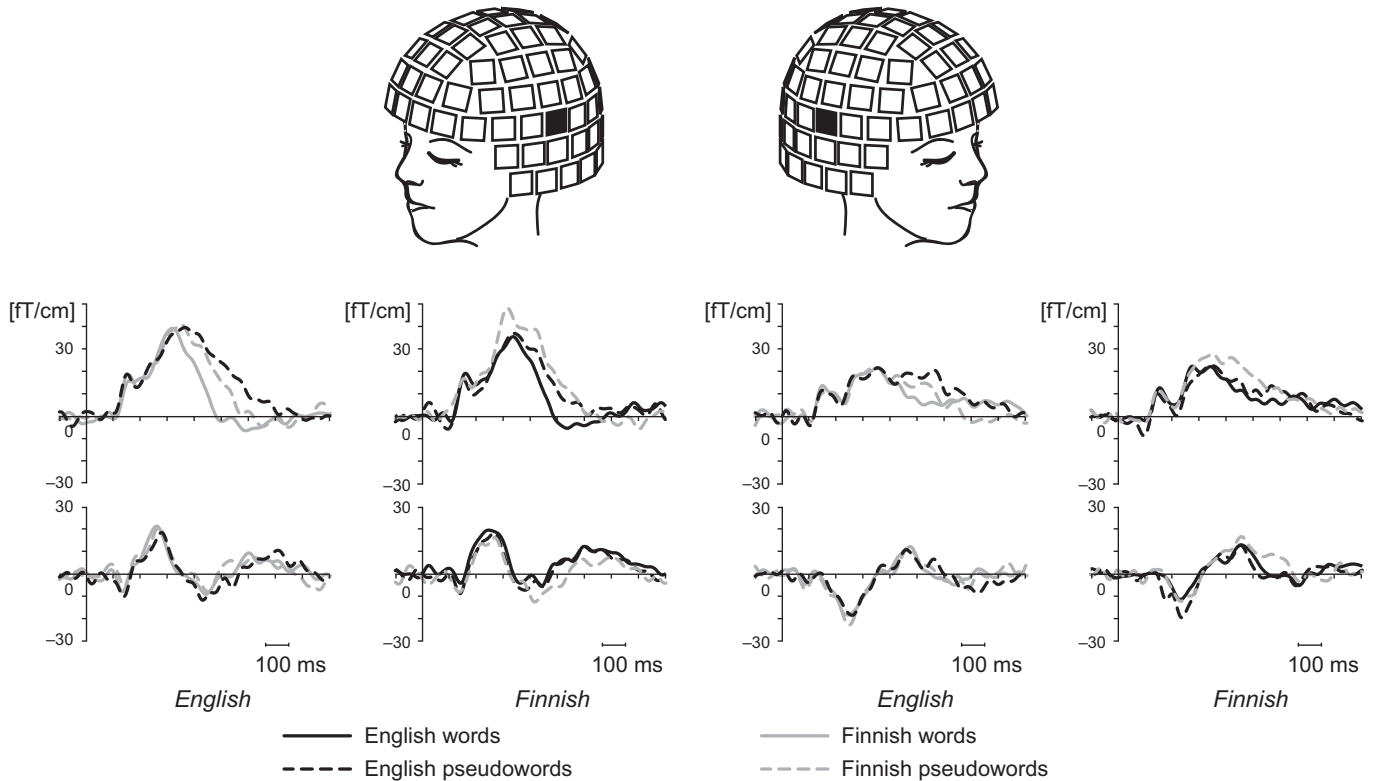


FIG. 4. Schematic illustration of the MEG sensor array and the grand average evoked responses to non-target stimuli detected by pairs of planar gradiometers over the left and right hemispheres during the English and Finnish tasks. The locations of the pairs of the planar gradiometers showing maximum signal are marked in black.

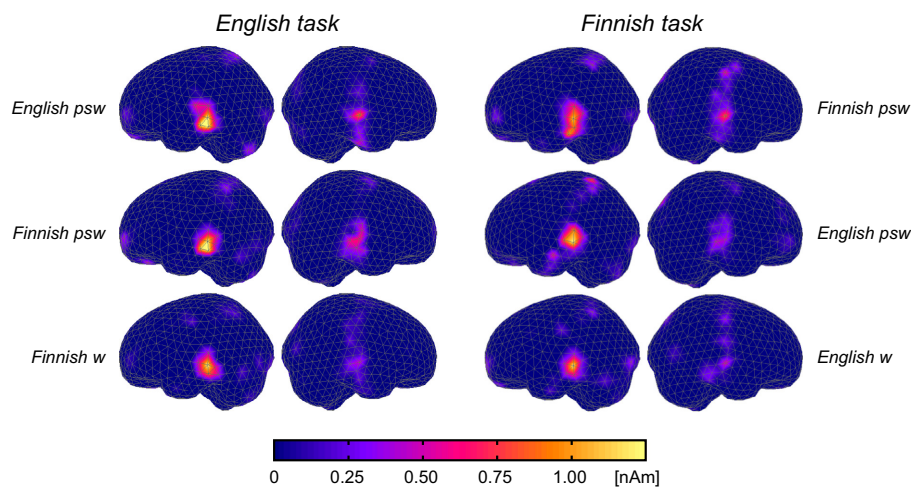


FIG. 5. Grand average minimum current estimates for the English and Finnish tasks during the N400 time interval (300–500 ms from the stimulus onset). Stronger activity over the temporal lobes is predominantly observed in the left hemisphere. psw, pseudowords; w, words. [Colour figure can be viewed at wileyonlinelibrary.com].

pseudowords containing no syntactic structure, no 'genuine', syntax-related P600 effects were expected. However, compelling evidence exists that the P600 is influenced by the probability of the occurrence of a syntactic violation and thus may be considered a member of the P3b family (Gunter *et al.*, 1997; Coulson *et al.*, 1998). In the present study, the probability of both types of pseudowords was equal, however, responses to English and Finnish pseudowords differed significantly depending on the task instructions. Furthermore, the probability of real words was twice as high as the probability of

pseudowords. If stimulus probability were an important factor modulating the evoked responses in the present study, the lowest-amplitude P600 would have been expected in response to words compared to pseudowords. However, the smallest P600 was observed in evoked potentials elicited by English pseudowords during the performance of the English task (Fig. 3B and D) suggesting that the effect of task was the most prevalent. The relative distribution of the ERP amplitudes across the experimental conditions, which was observed during the later time interval in the English

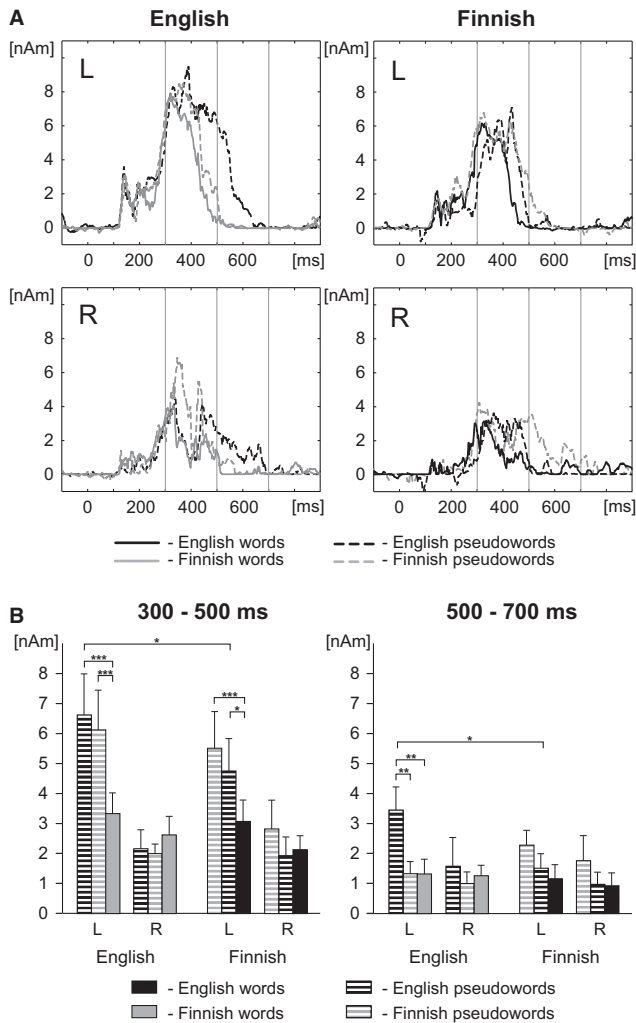


FIG. 6. (A) Grand average activation time courses of the left (L) and right (R) temporal sources obtained for the language tasks. Light vertical lines show the 300–500 and 500–700-ms time intervals. (B) Group mean amplitude of source activity \pm standard error of the mean (SEM) in the left (L) and right (R) hemisphere. The vertical lines indicate SEM, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

task, was similar to the distribution of amplitudes observed in the Finnish task during the earlier time interval. During the English task, the most negative response was elicited by English (task-language) pseudowords and during the Finnish task by Finnish pseudowords.

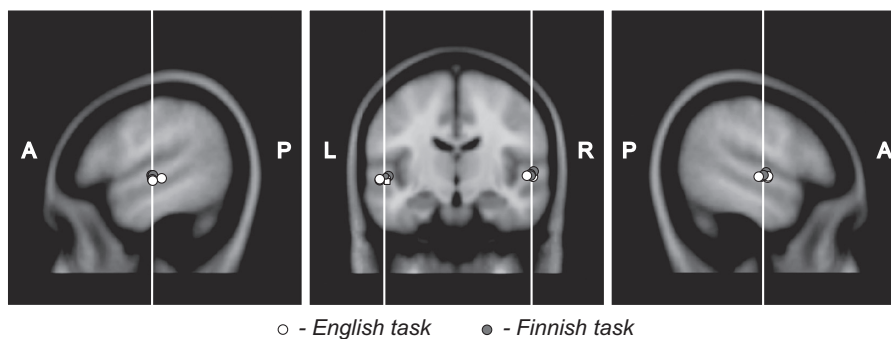


FIG. 7. Group average source locations of the N400 elicited by different stimulus types (task-language pseudowords, non-task-language pseudowords and non-task-language words) during the English and Finnish tasks overlaid on the standard averaged MRI.

However, despite a reliable demonstration of the N400 effects during both language tasks, the unequal proportion of words and pseudowords may be considered as a limitation of the present study, since it does not allow ruling out completely the possible effect of stimulus probability.

Another factor modulating the positive slow potentials is the type of behavioral response. For example, the P3b and PSW were shown to differ significantly between positive and negative probes, with the P3b being stronger for positive probes. The PSW, conversely, was stronger for negative probes (Pelosi *et al.*, 1998; Anurova *et al.*, 2005). The present study was designed to minimize the possible effect of the response type. Therefore, the potential N400 effects were only compared across the responses to non-target stimuli. Thus, the modulations of the evoked responses during the second time interval are rather caused by enhancement of negativity, or, in other words, the late N400 effect during the non-native language discrimination task, than by reduction of positivity.

The magnetic counterpart of the N400 was also modulated by task instructions, and all of the significant differences among stimulus types were observed exclusively in the left hemisphere. As with the N400 potential, the left-hemispheric source of its magnetic counterpart was activated more strongly by English pseudowords in the English than in the Finnish task. However, unlike the N400 potential, no significant difference between the magnetic fields elicited by the two types of pseudowords in the Finnish task was found. Both task-language and non-task language pseudowords activated the left-hemispheric source of the N400m to the same extent.

The differences between the electric and magnetic counterparts of the N400 may be, first of all, explained by different source configurations underlying these responses. While MEG preferentially measures the activity of superficial, tangentially oriented sources, EEG also obtains significant contributions from deep and radial sources (Lounasmaa *et al.*, 1996). The variety of factors modulating the N400 potential suggests that it is not a single component but rather a ‘family’ of brain responses reflecting several processes. This idea is further supported by topographic differences between studies and by the multiple sources reported for the N400 (Curran *et al.*, 1993; Halgren *et al.*, 2002; Marinkovic *et al.*, 2003; Silva-Pereyra *et al.*, 2003; Van Petten & Luka, 2006; Lau *et al.*, 2008, 2013, 2016). Though an equivalent current dipole for the N400m evoked by sentence-ending incongruent words (Simos *et al.*, 1997; Helenius *et al.*, 1998, 1999; Service *et al.*, 2007) or by word lists (Sekiguchi *et al.*, 2001) has consistently been localized to the left temporal lobe, additional sources were activated within the right temporal lobe. Halgren *et al.* (2002), employing extensive analysis of the N400m, confirmed the previously reported activation in the superior temporal

sulci strongly lateralized to the left hemisphere. However, a distributed source modeling technique also indicated activation of anteroventral temporal, orbitofrontal, and posteroventral prefrontal cortices in the left hemisphere and activation of the orbitofrontal and anterior temporal cortices in the right hemisphere. Source modeling of the MEG data in our study also revealed several activated areas, however, only those areas in the left and right temporal lobes that were consistently found in all subjects were chosen for further analysis. Thus, the N400m described in the present study reflects activation of local temporal sources – contrary with the N400 potential, which is a result of the summation of activation from broader areas. Furthermore, source modeling enabled the detection of the left lateralization of the N400m effects. The extensive N400 literature highlights the role of the left superior/middle temporal gyrus with neighboring areas being a candidate for storage of lexico-semantic representations (Patterson *et al.*, 2007; Lau *et al.*, 2008), although the cortical substrates for different aspects of language processing are far from clear. In the present study the N400m sources were located within the superior temporal sulcus and in adjacent areas including the superior and middle temporal gyri (STG and MTG). Although MEG is known to show activity originating preferentially from tangentially oriented sources, in practice this method can also register activity from brain convexities, because the sources located on the convexities often have a tilted orientation. That is why it is not surprising that, in some cases, sources of evoked fields are located on gyral surfaces. The important role of the STG in both visual and auditory language comprehension was shown in a combined MEG/electrocortical stimulation study (Simos *et al.*, 2000). Preoperative electrocortical stimulation mapping was performed in patients with intractable seizure disorder after their participation in an MEG study employing visual and auditory word recognition tasks. The results demonstrated considerable overlap of the areas involved in word recognition in both sensory modalities within the STG. When electrocortical stimulation was applied to the MEG-derived areas, the subjects' ability to read either words or pseudowords and to process spoken language was dramatically disrupted. Common activation of the left MTG during visual and auditory language comprehension was shown in an fMRI study by Buchweitz *et al.* (2009). It is worth pointing out that the coordinates of the N400m sources obtained in our study did not differ between the subjects' native and second languages. This finding is in line with results of an fMRI study by Kim *et al.* (1997). The study demonstrated that in the inferior frontal cortex of late bilinguals' language-sensitive regions corresponding to the second and native languages were segregated, however, in the temporal lobes native and second languages tended to be represented in common cortical areas.

The isolation of the activity of the local temporal sources revealed that while task-related differences in the amplitude of the evoked potentials were found in both language discrimination tasks, the amplitude of the left temporal source activity was modulated by task instructions exclusively during the performance of the English task. This finding suggests that native linguistic information is processed more automatically at the level of the association temporal cortex, whereas processing of non-native linguistic information requires the involvement of controlled processes which modulate activity in the temporal cortex and recruit additional neural resources for lexical retrieval.

Among cognitive processes that may account for elicitation of the N400 in the language tasks, there are two probable candidates. The first one is discrimination between the languages at the orthographical level and the second one is lexical search, necessary for discrimination between pseudowords and real words. In order to perform

language discrimination tasks, subjects had to decide whether the stimulus was a real word and whether it was English or Finnish, although not necessarily in this order. Since pseudowords had letter combinations typical of either language, subjects could first discriminate between the languages at the orthographical level and, in the case of the non-target language, immediately press the NO-button, and only in the case of the target language proceed to the lexical level to discriminate between real words and pseudowords. Fast behavioral responses to all non-target-language stimuli support this suggestion, even if the two discrimination processes have some temporal overlap. Thus, the longer RTs and increase of the N400 potential elicited by task-language pseudowords compared with non-task-language stimuli may reflect lexical search in addition to discrimination between languages. Alternatively, in the case of short and simple words, lexical decision-making can outpace the language discrimination process. Lexical search is terminated immediately upon word recognition, while the process of discriminating between languages continues. Semantic meaning may also have been processed for words, despite there being no such requirement in this study.

We predicted that in the present study the most prominent N400 effect would be observed in the most difficult experimental conditions in each task – discriminating between task-language words and task-language pseudowords. For the N400 potential this was indeed the case in both the language tasks, and it was also the case for the magnetic counterpart of the N400 in the English task. It has been shown that semantic or conceptual processing difficulty may enhance the N400 (Monetta *et al.*, 2003; Hubbard *et al.*, 2014). For example, in a semantic relatedness judgment task on vertically arranged pairs of words (Hubbard *et al.*, 2014), the N400 was shown to be enhanced for related word pairs presented in a spatial arrangement that mismatched the spatial relationship of their referents (e.g., basement written above the attic). In a semantic categorization task (Monetta *et al.*, 2003), subjects had to discriminate between animals and non-animals. Distracters (non-animals) and names of uncommon animals (e.g., jellyfish), considered to be difficult words, elicited more pronounced N400 responses than names of common animals (e.g., horse), which were considered to be easy words. The authors concluded that an augmented N400 in response to the more difficult words reflected an increase in the amount of required cognitive resources. However, the effect of word frequency, also known to affect the N400 (i.e., less frequent words elicit stronger N400), could not be separated from the task difficulty in the aforementioned study. In our experimental setup all types of pseudowords and non-task-language words may be considered to be distracters. In accordance with previous observations (Wydell *et al.*, 2003), the most prominent N400 was elicited by pseudowords. The task-language pseudowords that had the highest orthographic similarity to target words – and therefore being the most distractive stimuli – were the most difficult to categorize. This was reflected at both behavioral and neurophysiological levels. The target-language pseudowords were associated with longer RTs and lower performance accuracy (Fig. 2) as well as with larger amplitude of the N400 potential (Fig. 3B–D). However, since the type of pseudowords (Finnish or English) that elicited the most prominent N400 differed between the two language tasks, while the stimuli remained the same, the task type can be considered the most important factor modulating the N400.

In conclusion, the amplitude of both the electric and the magnetic counterparts of the N400 evoked by the same set of stimuli in the two language tasks was affected by task instructions implying that lexical judgment involves mechanisms of cognitive

control in addition to stimulus-driven automatic processes. Task-related modulations of the amplitude of the N400 potential were observed in both the English and the Finnish tasks, whereas activity of the left-hemispheric source of the N400m was affected by task instructions solely in the English task. This finding suggests that, at the level of the temporal cortex, native language is processed more automatically and that the controlled processing of linguistic information reflected in the electric N400 is accomplished by a broader neural network that extends beyond the association temporal areas.

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Conflict of interest

The authors declare no conflict of interest.

Author contributions

IA and PI contributed to the designing of the experiment and data collection. IA analyzed data and wrote the first draft; both coauthors reviewed and edited the manuscript submitted for peer review.

Data accessibility

The data used in this research was collected under provision of informed consent of the participants. Access to the data will be granted in line with that consent, subject to approval by the project ethics board and under a formal Data Sharing Agreement.

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