

Memory Traces for Words as Revealed by the Mismatch Negativity

Friedemann Pulvermüller,* Teija Kujala,† Yury Shtyrov,* Jaana Simola,† Hannu Tiitinen,† Paavo Alku,‡ Kimmo Alho,† Sami Martinkauppi,§ Risto J. Ilmoniemi,[¶] and Risto Näätänen^{†,¶}

*Cognition and Brain Sciences Unit, Medical Research Council, Cambridge CB2 2EF, United Kingdom; †Cognitive Brain Research Unit, University of Helsinki, 00014 Helsinki, Finland; ‡Laboratory of Acoustics, Helsinki University of Technology, 02015 HUT, Helsinki, Finland; and §Department of Radiology and ¶BioMag Laboratory, Medical Engineering Centre, Helsinki University Central Hospital, 00029 HUS Helsinki, Finland

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Brain responses to the same spoken syllable completing a Finnish word or a pseudo-word were studied. Native Finnish-speaking subjects were instructed to ignore the sound stimuli and watch a silent movie while the mismatch negativity (MMN), an automatic index of experience-dependent auditory memory traces, was recorded. The MMN to each syllable was larger when it completed a word than when it completed a pseudo-word. This enhancement, reaching its maximum amplitude at about 150 ms after the word's recognition point, did not occur in foreign subjects who did not know any Finnish. These results provide the first demonstration of the presence of memory traces for individual spoken words in the human brain. Using whole-head magnetoencephalography, the major intracranial source of this word-related MMN was found in the left superior temporal lobe. © 2001 Academic Press

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INTRODUCTION

The mismatch negativity (MMN),¹ a unique indicator of automatic cerebral processing of acoustic stimuli (Näätänen, 1990, 1995; Näätänen and Winkler, 1999), is elicited by infrequent deviant stimuli occasionally replacing frequently occurring, "standard," stimuli. It typically reaches its maximal amplitude at frontal and central sites of the scalp, with its main generators being located in the auditory cortex of each hemisphere. Reliable MMNs can be obtained even after hundreds of presentations of the same deviant stimu-

lus, given that it occurs at a low probability (<20%) among frequent (>80%) standards. Importantly, MMN elicitation is independent of the direction of the subjects' attention. Even if they ignore these stimuli, being engaged in other activities (for example in reading a book, playing a demanding computer game, or watching a movie), infrequent deviants elicit an MMN, suggesting that it is generated by an automatic, preattentive process (Näätänen, 1990, 1995; Näätänen and Winkler, 1999; Schröger, 1996).

Recently, the MMN was found to reflect the processing of acoustic and phonological properties of speech sounds also (Aaltonen *et al.*, 1997; Alho *et al.*, 1998; Kraus *et al.*, 1996; Sandridge and Boothroyd, 1996; Näätänen *et al.*, 1997). Vowels presented as deviant stimuli elicited considerably larger MMNs when they were prototypic members of a phonological category than when they were difficult to classify in the phonological system of the subject's native language. Consequently, the amplitude of the MMN obtained in such paradigms seems to reflect the activation of permanent speech-sound memory traces in the brain (Dehaene-Lambertz, 1997; Näätänen *et al.*, 1997; Cheour *et al.*, 1998; Näätänen, 2001). The present study extends this finding by demonstrating the existence of memory traces for whole words of the native language in the human brain.

MATERIALS AND METHODS

Design

First, two EEG experiments were performed. Words and pseudo-words, each consisting of two syllables, were acoustically presented to subjects instructed to watch a silent movie and ignore these sounds. In selecting the stimuli, we took advantage of a special property of the Finnish language, namely, that it comprises a certain type of geminate, so-called "double-stop consonants." These phonemes include a pause of ~200 ms as a phonological distinctive feature. These

¹ Abbreviations used: CV syllable, consonant-vowel syllable; ECD equivalent current dipole; EEG, electroencephalogram/electroencephalography; MEG, magnetoencephalogram/magnetoencephalography; MMNm, magnetic mismatch negativity; MMN, mismatch negativity.

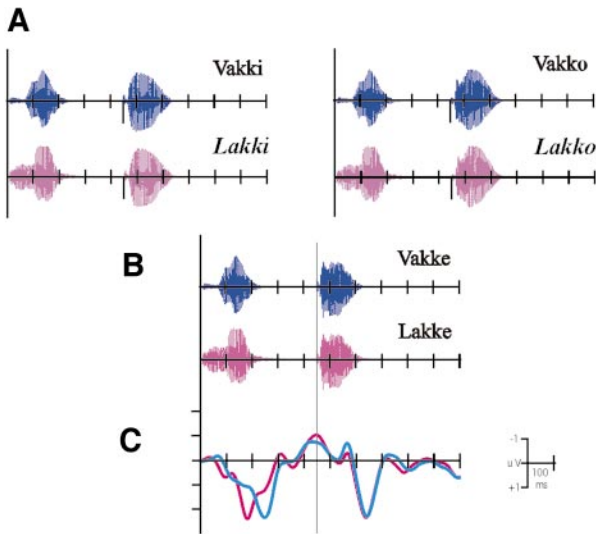


FIG. 1. Acoustic waveforms of deviant (A) and standard (B) stimuli presented in Experiments 1 (blue) and 2 (red). Meaningful words are given in italics. Each item consisted of two syllables separated by the long pause (>200 ms) characteristic of the Finnish double-stop consonants. (C) Brain responses elicited by the standard stimuli presented in Experiments 1 (blue) and 2 (red). The responses to the first syllables differed from each other in latency (reflecting the acoustic differences between /v/ and /l/).

phonemes are called “double consonants,” because in written Finnish, the pause before the actual plosion is coded by doubling of the consonant (e.g., “kk”). The long pause characterizing Finnish geminate stop consonants enables one to record separate brain responses to subsequent syllables even if naturally spoken language is used. In Experiments 1 and 2, two-syllabic stimuli were used with such a long pause between the syllables (Figs. 1A and 1B). We will call the first syllable of these stimuli the *context syllable* and the second the *critical syllable*. In Experiment 1, the critical syllables /ki/ and /ko/ were presented after the context syllable /va/, resulting in “vakki” and “vakko,” respectively, which are pseudo-words in Finnish. These pseudo-words served as deviant stimuli, each occurring with a 6% probability against the background of standards ending with the syllable “ke” (“vakke”). In Experiment 2, the identical critical syllables /ki/, /ko/, and /ke/ were presented after the context syllable /la/, now completing meaningful Finnish words, “*lakki*” (CAP) and “*lakko*” (STRIKE), and a pseudo-word, “*lakke*” (meaningful stimulus words are given in italics throughout). The two words served as deviant stimuli ($P = 6\%$), whereas the pseudo-word was used as the standard ($P = 88\%$).

Both experiments were first conducted with native speakers of Finnish and thereafter with foreigners who did not know any Finnish. Finally, whole-head magnetoencephalography (MEG) was used to localize the cor-

tical generators of the effect and thus, presumably, the memory traces for words (Experiments 3 and 4).

The MEG study reinvestigated the possible presence of a difference in the MMN elicited by words and pseudo-words. Now, an orthogonal design was used. One context syllable, /pa/, produced a word with one of the critical syllables, /ko/, but resulted in a pseudo-word together with the other critical syllable /ku/. The opposite was the case for the second context syllable, /ta/, which produced a word only with /ku/. As in the earlier experiments, the acoustic signals of the context and critical syllables were separated by the pause characterizing the Finnish geminate stops. The different designs are illustrated in Table 1. The reason for changing the design was to rule out the possibility that the physical properties of the context syllable itself contributed to any physiological differences between words and pseudo-words.

Experiments 1 and 2 (EEG)

Subjects

Nine healthy right-handed native Finnish speakers (age 20–30 years, mean 24) with normal hearing participated in both EEG experiments. Handedness was assessed by a short version (6 items) of the Edinburgh Handedness Inventory (Oldfield, 1971). None of the subjects had left-handed family members.

Experiments 1 and 2 were repeated with five subjects who did not know any Finnish. The native language of these control subjects was Russian or German. They, too, were right-handed and their age range (20–30 years) was identical to that of the Finnish group.

Stimuli

Finnish words and pseudo-words, each consisting of two consonant-vowel (CV) syllables were selected. The first phoneme of each of the second syllables was a double-stop consonant, a voiceless stop after a pause of at least 200 ms (see Fig. 1). These language sounds are ideal for the present purpose, for they allow the recording of separate brain responses to subsequent syllables in continuous speech without component overlap.

A native female Finnish speaker spoke a long series of the bisyllabic words “*vakka*” and “*lakka*” and random sequences of CV syllables including /ki/, /ko/, and /ke/. The material was recorded in a sound-proof room and sampled at 30,000 Hz.

From more than 50 exemplars of each type, the context syllables (/va/, /la/) and critical syllables (/ke/, /ki/, /ko/) were selected according to phonetic and phonological criteria as follows. (1) The F0 frequencies of the vowels of the critical syllables differed no more than 3% from each other; (2) the voice-onset times of all syllable-initial stops were between

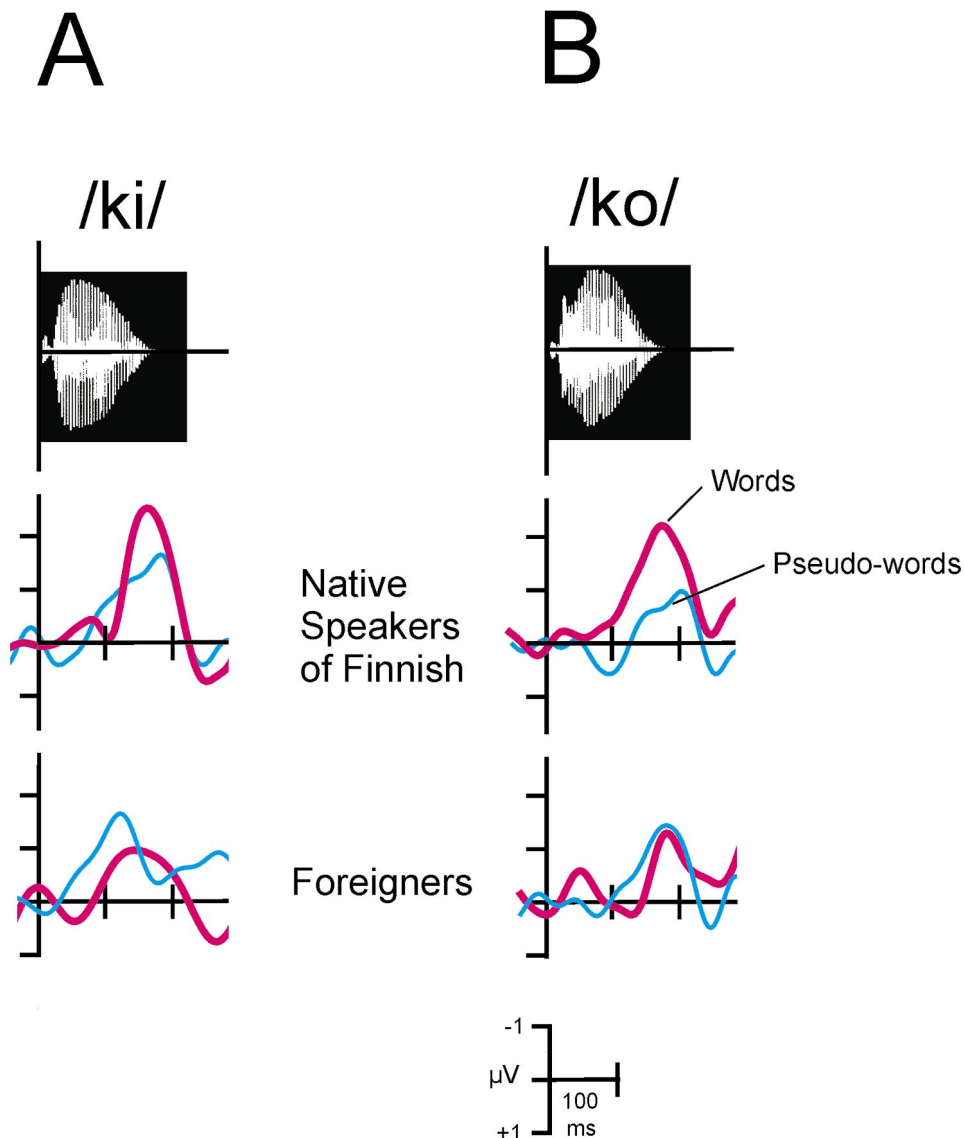


FIG. 2. Mismatch negativities (MMNs) elicited by the critical syllables /ki/ (A) and /ko/ (B) when placed in a word context (red traces) and in a pseudo-word context (blue). The acoustic waveforms of the stimuli which elicited the MMNs are shown at the top. Data from Finnish speakers are presented in the upper plots, those from foreigners appear at the bottom. A word-related MMN enhancement occurred in Finnish speakers but not in foreigners.

15 and 20 ms; (3) all vowels were prototypical members of their respective phonological categories. The syllables from each category were shortened to the same length (250 ms for the context, 230 ms for the critical syllables) and normalized to the same peak sound energy. These CV syllables, separated by a pause of >200 ms in each case, were combined to yield the stimuli presented in Fig. 1.

Before the experiment, the point in time at which the word stimuli could actually be recognized was determined. For this purpose, fragments of each stimulus were generated including the first (context) syllable plus the initial 10, 20, 30, 40, 50, 60, 70, or 80 ms of the second (critical) syllable. For each stimulus fragment,

four native speakers were asked to name the second syllable and to indicate whether they could identify a meaningful Finnish word. All subjects correctly identified each of the second syllables when being presented with the 30-ms fragments, showing correct word recognition for these fragments as well. Thus, the recognition point (Marslen-Wilson, 1987) of the present two words was at 30 ms from the onset of their second syllable. Furthermore, in Finnish, there are no alternative words starting with “*lakki-*” and “*lakko-*” (except for compounds including these morphemes). Therefore, their word uniqueness point can also be located at around 30 ms after the /ki/ or /ko/ onset, respectively.

TABLE 1
Designs of EEG and MEG Experiments

Experiments 1 and 2 EEG (2-syllabic stimuli)	Deviant: critical 2nd syllable, $P = 0.06$		Standard, $P = 0.88$
	/ki/	/ko/	/ke/
Expt 1 Context 1st syllable /va/, $P = 1$	Pseudo-word, Vakki	Pseudo-word, Vakko	Pseudo-word, Vakke
Expt 2 Context 1st syllable /la/, $P = 1$	Word, Lakki	Word, Lakko	Pseudo-word, Lakke
Experiments 3 and 4 MEG (1-syllabic stimuli)	Deviant: critical 2nd syllable, $P = 0.16$		
	Expt 3 /ko/	Expt 4 /ku/	
Context 1st syllable /pa/, $P = 0.42$	Word, Pakko	Pseudo-word, Pakku	
Context 1st syllable /ta/, $P = 0.42$	Pseudo-word, Takko	Word, Takku	

Note. Stimuli are listed together with their probability of occurrence in all four experiments. Critical syllables are written in italics if they occurred in word contexts and in normal font if they occurred in pseudo-word contexts.

Procedure

During the EEG recording, subjects, instructed to ignore the acoustic stimuli, watched self-selected silent movies in an electrically shielded and dimly lit sound-proof room. The order of the experiments was counterbalanced across the subjects and within each experiment; the order of the stimulus blocks was counterbalanced as well. Bisyllabic stimuli were presented through headphones with a stimulus onset asynchrony (SOA) of 1200 ms. Loudness was adjusted to 50 dB above the individual hearing threshold. In each experiment, 160 tokens of each deviant and 2720 standards were delivered. Stimuli were presented in four blocks in each experiment with different pseudo-randomized stimulus sequences.

EEG Recording

The EEG was recorded with 64 Ag/AgCl electrodes montaged in a cap (Virtanen *et al.*, 1996) against a reference at the tip of the nose. The horizontal and vertical electro-oculograms were recorded through two additional electrode pairs placed close to the eyes. DC signals (0–100 Hz) were continuously recorded using the SynAmps/NeuroScan system and sampled at 200 Hz.

Data Analysis

Epochs of 600 ms duration, starting 50 ms before the onset of the critical stimulus, were obtained from the continuous signals. Trials with eye artifacts (>75 – 100 μ V) were rejected. Separate stimulus-triggered ERPs were calculated for the standard and for each of the deviants. For calculating MMNs, the standard-stimulus averages were subtracted from the respective deviant-stimulus averages. For statistical analysis, the average values of the MMN curves were calculated for the interval 150–180 ms from critical-syllable onset,

which were then compared between the different stimulus types using analyses of variance.

Experiments 3 and 4 (MEG)

These experiments resembled the EEG experiments, with exceptions as follows: Twelve new right-handed native speakers of Finnish (age 20–32 years, mean 26) were employed. In this case, the stimuli (generated according to the method described above) were the single syllables /pa/, /ta/, /ko/, and /ku/, which were randomized and presented with a constant SOA of 450 ms so that any two syllables were again separated by the long pause characterizing the Finnish geminate stops. This yielded either meaningful or meaningless syllable combinations. In Experiment 3, /pa/ and /ta/ were the standard stimuli ($P = 42\%$ each) and the deviant stimulus was /ko/, which completed a meaningful Finnish word when following /pa/ (“pakko”—COMPULSION, CONSTRAINT), whereas when following the other standard, /ta/, the pseudo-word “takko” resulted. In Experiment 4, the same standards, /pa/ and /ta/, were used together with the deviant stimulus /ku/, yielding the pseudo-word “pakku” and the word “takku” (TANGLE) in the two possible contexts (cf. Table 1). Note again that the long SOA of 450 ms implies a long (>200 ms) silent period between syllables.

TABLE 2

The MMN Amplitudes (in μ V) for the Critical Second Syllables in Experiments 1 and 2

Critical (2nd) syllables:	/ki/	/ko/
Expt 1: Context (1st) syllable /va/	–1.4	–0.7
Expt 2: Context (1st) syllable /la/	–2.6	–2.0

Note. The MMN amplitude is enhanced (italics) when words, rather than pseudo-words, were used.

bles, guaranteeing that double-stop consonants were perceived. This was confirmed by each of the subjects. At least 100 artifact-free MEG epochs were required from each subject and for each deviant-in-context.

Data were recorded using a 122-channel whole-head gradiometer (Neuromag Ltd.). The magnetic counterpart of the mismatch negativity, called the MMNm, was calculated for each deviant-in-context, by subtracting its physiological response from the average of the responses to the two standards. Preliminary analyses ascertained that the two standards did not significantly differ from each other in their MEG responses. Equivalent current dipoles (ECDs) were calculated for individual subjects on the basis of the MMNm data from 34 channels covering the perisylvian areas of the left and right hemisphere, respectively. Statistical comparisons were performed on data recorded with these channels. At the other locations, there was no indication of a significant and consistent difference between physiological responses to words and pseudo-words.

RESULTS

In Experiments 1 and 2, the critical syllables completing words elicited significantly larger MMNs than those elicited by the same syllables when they completed pseudo-words, $F(1,8) = 13.2$, $P < 0.007$ (Table 2, Fig. 2). Additional statistical analyses were performed on data from 16 electrodes at the central, occipital, and left and right perisylvian sites. These analyses confirmed the main effect of context, $F(1,8) = 7.6$, $P < 0.02$, and also revealed a significant interaction indicating that the difference was largest at the frontocentral recordings (Fz, Cz, and the adjacent sites), $F(1,8) = 12.0$, $P < 0.009$.

No differences between the word and pseudo-word contexts were seen in the control group of subjects who did not know any Finnish. The grand-average waveforms gave no indication of even a tendency toward a MMN enhancement in word contexts. Figure 2 shows that the native Finnish speakers exhibited the MMN enhancement for words, whereas for the foreigners with no command of Finnish no such effect was obtained. Thus, mismatch responses were enhanced when syllables completed words in the subjects' own language, but there was no indication of a similar effect in subjects who did not know the language.

The MEG Experiments 3 and 4 revealed that the neuromagnetic correlate of the MMN, the MMNm, was also enhanced in amplitude in response to syllables placed in a word context compared with that elicited by the same syllables placed in pseudo-words, $F(1,11) = 16.4$, $P < 0.002$ (Figs. 3 and 4, Table 3). The 122-channel gradiometer recorded the strongest signals above the posterior part of the left Sylvian fissure (Fig. 3).

This result from the MEG study was confirmed by the analysis of ECDs calculated separately for the peak dipole moments obtained from the left and right hemisphere, respectively, between 150 and 240 ms from stimulus onset. The dipole moments for both the words and the pseudo-words were generally greater on the left than on the right, $F(1,11) = 15.4$, $P < 0.002$ (21 vs 13 nA), suggesting that the main source of the effect was in the left hemisphere. Since the average goodness of fit of the dipoles was greatest on the left side, $F(1,11) = 11.5$, $P < 0.003$, these dipoles were analyzed separately. Only left-hemispheric peak dipole moments were significantly greater for words than for pseudo-words, $F(1,11) = 5.0$, $P < 0.05$ (24 vs 19 nA), whereas a similar effect could not be found for the data recorded from the right hemisphere ($F < 1$).

An additional overall analysis was performed in which dipoles with low goodness of fit (cut-off = 70%) were replaced by zero values. This strategy was earlier used by Shtyrov *et al.* (2000) to rule out the possibility of a contribution of noise-related artifacts. When dipole moments calculated for both hemispheres were entered into one repeated-measures analysis of variance (Syllable \times Wordness \times Hemisphere), the main effects of Hemisphere, $F(1,11) = 25.3$, $P < 0.0004$, and Wordness, $F(1,11) = 5.6$, $P < 0.03$, again became manifest. As in the earlier analysis, left-hemispheric dipoles were significantly greater for words than for pseudo-words, $F(1,11) = 5.5$, $P < 0.04$, but there was no comparable effect for the sources on the right ($F = 0.2$). The Hemisphere \times Wordness interaction just failed to reach significance ($F = 2.8$, $P = 0.1$). Thus, we found once again evidence for MMNm enhancement if syllables are presented in word context. While there is good support for a left-hemispheric contribution to this effect, strong statements about the right-hemisphere's role are not possible based on the present set of analyses.

Single-dipole modeling performed on the data of individual subjects located the main generator of the word-elicited MMNm in the superior temporal lobe (Fig. 5). In the 12 subjects employed, the left-hemispheric single dipoles explained, on average, 81% of the variance. The present findings agree with the previous ones (e.g., Shtyrov *et al.*, 1998, 2000; see also Näätänen *et al.*, 1997), indicating that the ECDs calculated from MMNms elicited by meaningless spoken syllables are located in these same areas with, in noise-free environments, lateralization to the left. Figure 5B further indicates that the sources were more anterior in the right hemisphere than in the left, but this difference observed previously for the MMNm and other MEG responses to simple tone stimuli (Alho *et al.*, 1998b) presumably relates to anatomical hemispheric asymmetries.

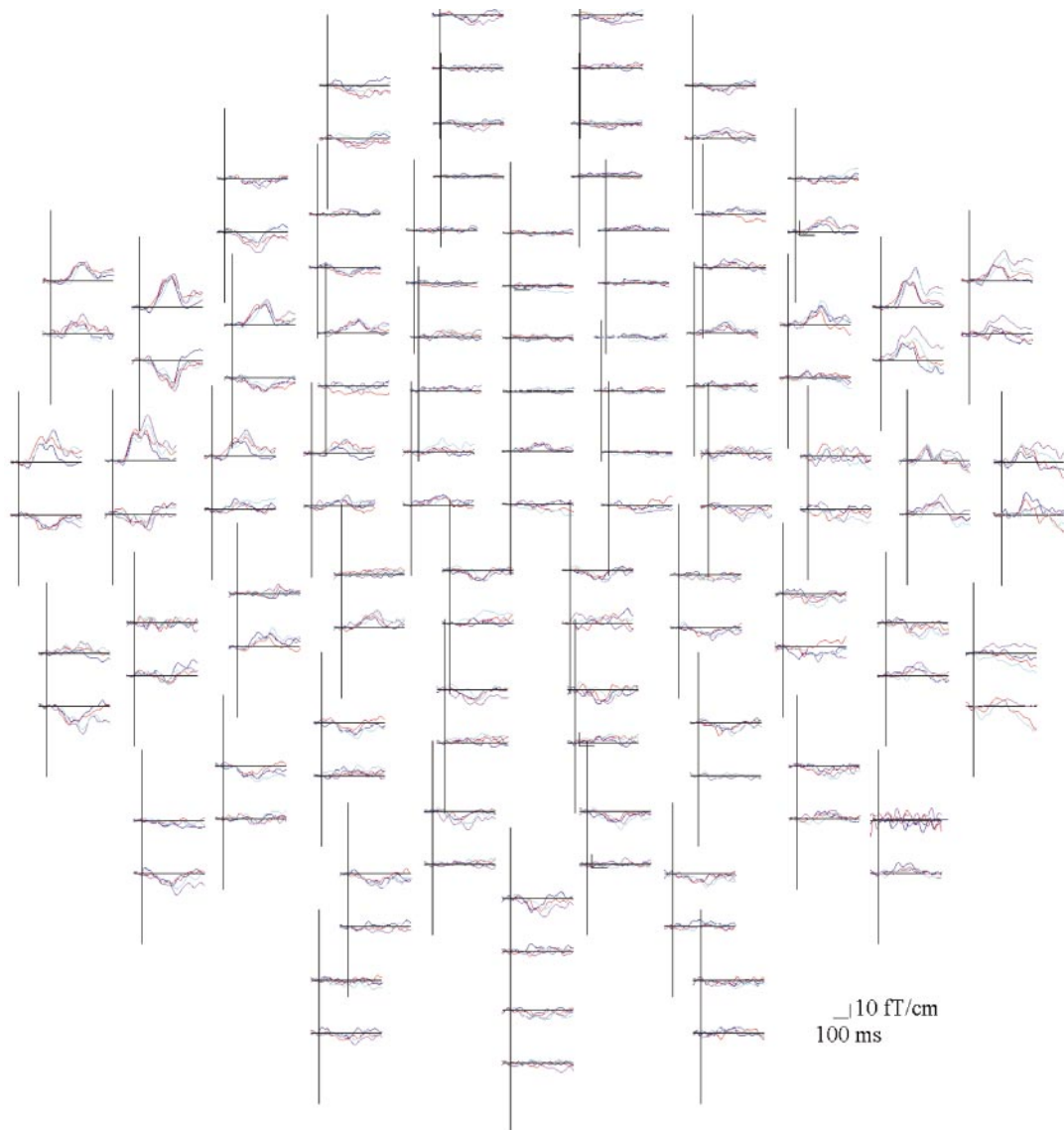


FIG. 3. Whole-head neuromagnetic mismatch response (MMNm) to words and pseudo-words. MMNm elicited by the syllable /ko/ is shown in bluish green and purple and those elicited by /ku/ are in blue and red. Reddish colors indicate word responses. It can be seen that the maximal field gradients were obtained at the left- and right-lateral sites. Statistical analyses of dipole moments revealed stronger sources on the left than on the right and stronger dipole moments for words than for pseudo-words (see text).

DISCUSSION

In the present series of four experiments performed with native speakers of Finnish, we obtained mismatch negativities, MMNs and MMNms, of a higher amplitude to syllables placed in a word context than in a meaningless pseudo-word context, suggesting that the MMN(m) can reflect the activation of neuronal memory traces for words.

Since exactly the same stimuli were presented as the second and critical syllables of words and pseudo-words, the enhancement of the MMN and MMNm cannot be due to physical differences between the stimuli eliciting these responses. The identity of the

critical second syllables in the words and pseudo-words of all four experiments also rules out the frequency of occurrence of individual phonemes or syllables as an explanation of the enhancement of the MMN(m). Furthermore, a long-latency effect of the context (first) syllables—/va/ or /la/ in the EEG experiments—could not have caused the effect, as there was no such long-latency effect (cf. Fig. 1C). It appears to be the interplay between the context and the critical syllables of words that underlies the MMN enhancement observed. This is even clearer in Experiments 3 and 4 in which a crossover design was used (cf. Table 1). In these MEG experiments, one

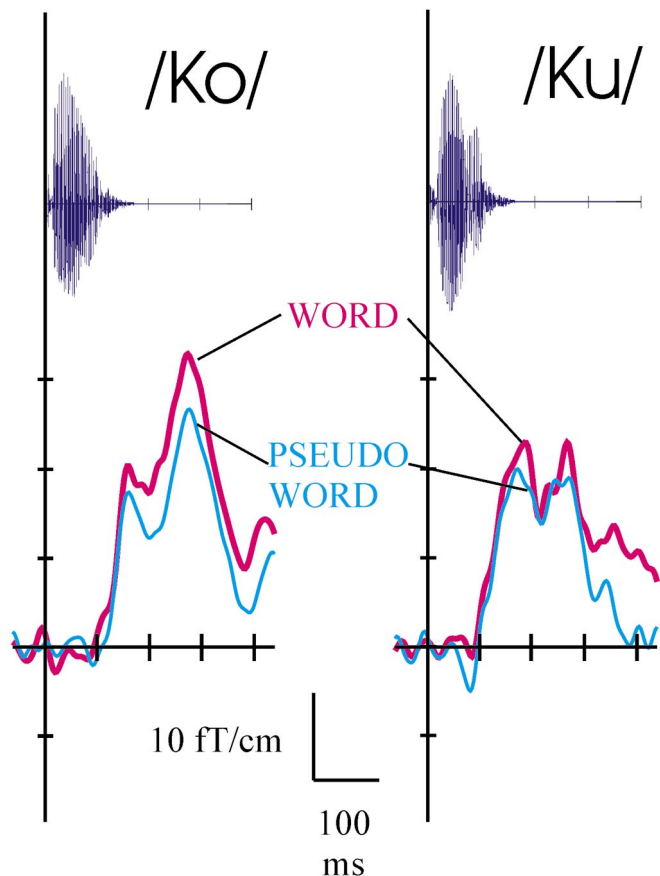


FIG. 4. Mismatch fields elicited by syllables in word vs pseudo-word contexts. MMNm response to the final and critical syllables of words and pseudo-words recorded over the left Sylvian fissure. Words elicited larger amplitudes of the MMNm than did pseudo-words.

context syllable, /pa/, produced a word with the critical syllable /ko/ (“*pakko*”) and a pseudo-word with the other critical syllable, /ku/ (“*pakku*”), whereas the opposite was the case for the other context syllable, /ta/ (“*takko*” vs “*takku*,” respectively). Therefore, it is not possible to explain the MMN(m) enhancement for words by a long-latency effect elicited by the context syllables alone. Thus, the sequential

TABLE 3

The MMNm Amplitudes (in fT/cm) for the Critical Second Syllables in Experiments 3 and 4, in Which an Orthogonal Design Was Used (cf. Table 1)

Critical (2nd) syllables:	/ko/	/ku/
Expt 1: Context (1st) syllable /pa/	<i>28.3</i>	20.9
Expt 2: Context (1st) syllable /ta/	23.2	<i>24.0</i>

Note. The MMNm amplitudes for each syllable were enhanced when presented in word context (italics) rather than pseudo-word context. /ko/ produces a Finnish word if presented after /pa/, and /ku/ yields a word after /ta/ (SOA = 450 ms).

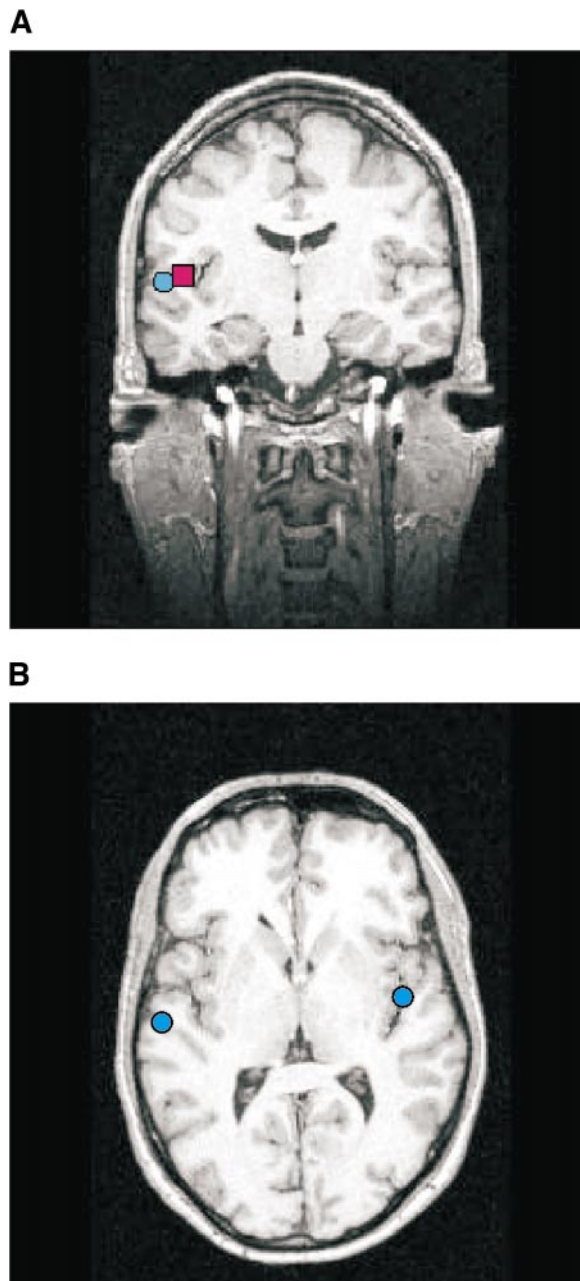


FIG. 5. (A) The main sources of the word- and pseudo-word-elicited MMNms were localized in the superior temporal lobe of the left hemisphere (single-subject data: goodness of fit 86.5%, confidence volume 82 mm³; left is left on all scans). The equivalent current dipole (ECD) locations did not significantly differ between words (square) and pseudo-words (circle). (B) ECD modeling of the left- and right-hemispheric sources of the MMNm elicited by pseudo-words. Note the slightly anterior right-hemispheric source compared to its left-hemispheric counterpart. Word- and pseudo-word-evoked dipole sources appeared at similar locations.

alignment of these syllables resulting in a word was crucial.

One could argue that the conditional probability of the successive phonemes might have been relevant for the occurrence of the effect. For example, the frequen-

cies of phoneme triplets (Wickelgren, 1969) may differ between “vak” and “lak,” and any physiological difference between “vakki” and “lakki” may therefore be confounded by differences in trigram frequencies. Again, however, the results from the MEG experiments rule out this possibility. Due to the orthogonal design used in Experiments 3 and 4 (Table 1), any difference in trigram frequencies working in favor of a word response for one of the word/pseudo-word pairs must necessarily work in the opposite direction for the other pair. For instance, if “pak” were more frequent than “tak,” this could be an advantage to both the word “pakko” and the pseudo-word “pakku,” but would then also be a disadvantage for both the pseudo-word “takko” and the word “takku,” and the same point can be made with regard to all phoneme trigrams in the stimulus sets. Therefore, given the present experimental design a physiological response difference between words and pseudo-words could not be caused by differential trigram frequencies.

Nevertheless, if two syllables form a word, then they must frequently occur in succession, whereas if two syllables form a pseudo-word, they may never, or only extremely rarely, occur in direct succession. One might therefore ask whether the co-occurrence or correlation statistics of the two syllables included in the stimulus words and pseudo-words was the relevant factor reflected in the MMN amplitude, rather than their word or pseudo-word property per se. Our interpretation would be compatible with this view. Only in the case of frequently occurring sequences, such as the phoneme and syllable sequences that represent words of a language, is it possible for the CNS to build up a neuronal representation. Such a build-up of representations that serve as the substrates of recognition and memory follows from Hebbian associative learning principles (Braitenberg and Pulvermüller, 1992; Pulvermüller, 1996, 1999). Thus, if a syllable combination is a word, it is necessarily characterized by an enhanced conditional probability of its component syllables.

We acknowledge the possibility of finding syllable pairs that do not make up words in a given language but nevertheless frequently follow each other in language use. This is particularly obvious for certain sequences of function words (e.g., “into the,” “as well,” Redlich, 1993) and for inflectional or derivations morphemes (-ation, -ity) and their sequences (-edness, -ishly). Future experiments should determine whether high conditional probabilities of two syllables alone can also result in an MMN enhancement similar to the one found here for consecutive syllables forming meaningful words.

The present data set suggests that the frequency of use of word stimuli might have been related to the physiological response. In both EEG and MEG experiments, the word stimuli differed in their frequencies of occurrence in standard spoken and written text. The

database of Saukkonen *et al.* (1979) indicates normative lexical frequencies of 7 vs 54 occurrences per million for the words “lakki” and “lakko,” respectively, which were used as stimuli in the EEG experiments. Similarly, one of the words in the MEG studies, “pakko,” has high word frequency (125 per million according to Saukkonen *et al.*, 1979) while the other, “takku,” is so rarely used that it did not occur in the analyzed sample (frequency <3 per million). Figures 2 and 4 indicate that, in both sets of experiments, the enhancement of the MMN and MMNm, respectively, was somewhat larger for the word with higher word frequency. Although statistical analyses did not confirm such amplitude differences, one may take this as a hint of a possible contribution of the probability with which two syllables follow each other to the observed effect. We should, however, note that a significant MMN enhancement was also seen for the low-frequency words, therefore suggesting that the effect can be present even if a syllable combination does not occur frequently. Future research should aim at more precisely defining the possible contribution of the lexical status (word vs pseudo-word), word frequency, and conditional probabilities of phonemes and syllables to the brain’s mismatch response.

The ERP recordings showed the typical frontocentral maximum of the MMN; dipole localization performed on the MEG data provided evidence for the superior temporal main sources, which characterize the magnetic counterpart of this component. These typical MMN and MMNm topographies can be explained by very similar sets of cortical generators (Näätänen and Winkler, 1999). The present MEG experiments documented a stronger activation of the left hemisphere compared with that of the right. The critical second syllables generally produced stronger dipole moments on the left than on the right. Furthermore, the neuro-magnetic word–pseudo-word difference became manifest in the recordings and dipole moments obtained for the dominant left hemisphere and, in addition, in the analysis of pooled data from both hemispheres. The recordings from the right hemisphere analyzed separately did not document a similar effect. However, we emphasize that our data do not exclude the possibility of additional right-hemispheric generators contributing to word and pseudo-word processing or to the word-specific enhancement of the MMNm. Also, no clear left-laterality of MMNs was obvious from the EEG study. Therefore, the laterality question should be re-addressed in future research. It may well turn out that the laterality of the word-related MMN strongly depends on the experimental setting and, in particular, on the stimulus words chosen. Differential left- and right-hemispheric involvement in the processing of words from different categories has been reported in earlier neuroimaging work (see Pulvermüller, 1999, for a review).

The enhancement of the MMN and MMNm may indicate an enhancement of brain activity induced by word stimuli relative to that elicited by pseudo-words. This word-related activation may be caused by the stored long-term memory traces of words. It has been proposed that these memory traces are organized as strongly connected assemblies of cortical neurons which become fully active, or "ignite," when words are being processed (for discussion, see Pulvermüller, 1999). After the presentation of a pseudo-word that does not occur in the usual language input, the ignition process would fail to emerge. Importantly, the present set of experiments demonstrates that, for memory traces of words to be activated, it is not necessary to actively direct attention to the incoming stimuli; in this sense, memory traces of spoken words are activated preattentively.

The relevant differences between word and pseudo-word contexts emerged already at around 150 ms after the earliest point in time when the words could be recognized on the basis of the acoustic input (word recognition point; Marslen-Wilson, 1987). This is consistent with recent results indicating that the neuronal counterparts of words become active early, within the first quarter of a second after the relevant information occurs in the input (e.g., Dehaene, 1995; Müller and Kutas, 1996; Pulvermüller *et al.*, 1995, 1999; Skrandies, 1998).

The latencies, topographies, and dipole loci obtained in the four experiments leave no doubt that an MMN(m) response was registered to naturally spoken words and pseudo-words. One may, however, ask whether the enhancement of the mismatch responses crucially depends on the low probabilities with which the word and pseudo-word deviant stimuli were presented in the experiment ($P < 0.2$). The answer is yes: There are numerous studies looking at physiological responses to equiprobable words and pseudo-words. These studies converge on the finding that a relatively late brain response (latency ~ 400 ms) is larger for pseudo-words than for words (e.g., Holcomb and Neville, 1990; Pulvermüller *et al.*, 1995). The present effect is different in three respects: (a) considerably shorter latency (150–200 ms), (b) cortical topography (frontal maximum), and (c) direction (larger negativity to words in the present study vs larger negativity to pseudo-words in the previous studies). Furthermore, Diesch *et al.* (1998) compared word and pseudo-word standards with a high probability of occurrence (80%) and found stronger dipole moments for pseudo-words than for words, again the opposite of the present effect. We can thus conclude that the present effect crucially depends on the procedure applied, in particular the low stimulus probability of the word and pseudo-word deviants in the experiment. Clearly, the present MMN enhancement for words reflects an earlier process compared with the differences revealed by the majority of

the previous studies of word and pseudo-word processing.

CONCLUSION

Spoken words from the subjects' native language elicited a larger neurophysiological mismatch response, the electric mismatch negativity, and its magnetic equivalent compared with pseudo-words not occurring in the usual language input. This mismatch-response enhancement for words occurred even though subjects were instructed to ignore the word stimuli and focus their attention elsewhere. This enhancement of the mismatch response after word presentation demonstrates the existence of memory traces for words of the subjects' language. The activation of these memory traces does not require focused attention to stimuli. Previous findings have established that the MMN reflects neuronal memory traces of language sounds, phonemes (Dehaene-Lambertz, 1997; Näätänen *et al.*, 1997). The present study now extends this result from the level of single phonemes to that of meaningful language units, morphemes, and whole words. Consequently, it appears that, at the different linguistic levels, the automatic access to stored language representations leads to the enhancement of the cortical mismatch response.

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