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Determinants of dominance: Is language laterality explained by physical or linguistic features of speech?

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The nature of cerebral asymmetry of the language function is still not fully understood. Two main views are that laterality is best explained (1) by left cortical specialization for the processing of spectrally rich and rapidly changing sounds, and (2) by a predisposition of one hemisphere to develop a module for phonemes. We tested both of these views by investigating magnetic brain responses to the same brief acoustic stimulus, placed in contexts where it was perceived either as a noise burst with no resemblance of speech, or as a native language sound being part of a meaningless pseudoword. In further experiments, the same acoustic element was placed in the context of words. We found reliable left hemispheric dominance only when the sound was placed in word context. These results, obtained in a passive odd-ball paradigm, suggest that neither physical properties nor phoneme status of a sound are sufficient for laterality. In order to elicit left lateralized cortical activation in normal right-handed individuals, a rapidly changing spectrally rich sound with phoneme status needs to be placed in the context of frequently encountered larger language elements, such as words. This demonstrates that language laterality is bound to the processing of sounds as units of frequently occurring meaningful items and can thus be linked to the processes of learning and memory trace formation for such items rather than to their physical or phonological properties.

Keywords: Speech; Sound; Word; Language; Auditory; Cortex; Hemisphere; Perception; Asymmetry (lateralization, laterality); Event-related (ERP, ERF); Magnetoencephalography; Mismatch negativity (MMN, mismatch field, MMF, MMNm); Human

Introduction

Since its first description in the late 19th century (Broca, 1861; Wernicke, 1874), language laterality in the human brain has never been fully understood. Right-handed individuals, whose first-order relatives are also right-handers, have an overwhelmingly high probability of having their language circuits lateralized to the left hemisphere (Hugdahl, 2000; Josse and Tzourio-Mazoyer, 2004). This means that a stroke to their left “dominant” hemisphere will likely leave them with a neurological language deficit or aphasia whereas a lesion in the right hemisphere will in most cases not be associated with a language deficit (Dronkers et al., 2004). Also, the brain is activated more strongly on the left side than on the right one when right-handed subjects engage in language tasks (Price, 2001; Tervaniemi and Hugdahl, 2003), and even when they are exposed to language they do not attend to (Pulvermüller et al., 2004; Shtyrov et al., 2003).

One main theory, which we here call the acoustic laterality theory, postulates that the physical properties of speech sounds are essential factors determining laterality to the left. Language sounds are spectrally rich and occupy a wide band of frequencies between a few hundreds and some thousands of hertz. In addition, some language sounds change rapidly over time. Stop consonants (such as [t], [p], or [k]), for example, can be realized as a brief plosion occurring after a silent period of defined length at the end of syllables. In this view, rapidly changing sounds are preferentially processed by the left dominant hemisphere, whereas tonal patterns that change slowly activate the right hemisphere more strongly than the left one (Fitch et al., 1997; Tallal et al., 1993; Zatorre and Belin, 2001; Zatorre et al., 2002). This acoustic theory explains a range of behavioral data according to which the right ear predominantly connected to the left hemisphere has an advantage in perceiving sounds with rapid changes. Such evidence comes from dichotic listening studies showing the so-called right ear advantage (REA) for CV syllables, plosive stop consonants, and even non-speech sounds with rapid transitions and high-frequency components, whereas vowels, fricatives, and slow acoustic transitions demonstrated a reduced or abolished REA (Deutsch, 1974; Fitch et al., 1993; Halperin et al., 1973; Schwartz and Tallal, 1980; Shankweiler and Studdert-Kennedy, 1967; Spellacy and Blumstein, 1970; Studdert-Kennedy and Shankweiler, 1970; Weiss and House, 1973). The idea of laterality for rapidly changing sounds also finds support in brain imaging studies (Belin et al., 1998; Celsis et al., 1999a,b; Fiez et al., 1995; Jaramillo et al., 2001; Johnsrude et al., 1997). However, this explanation on the basis of physical features

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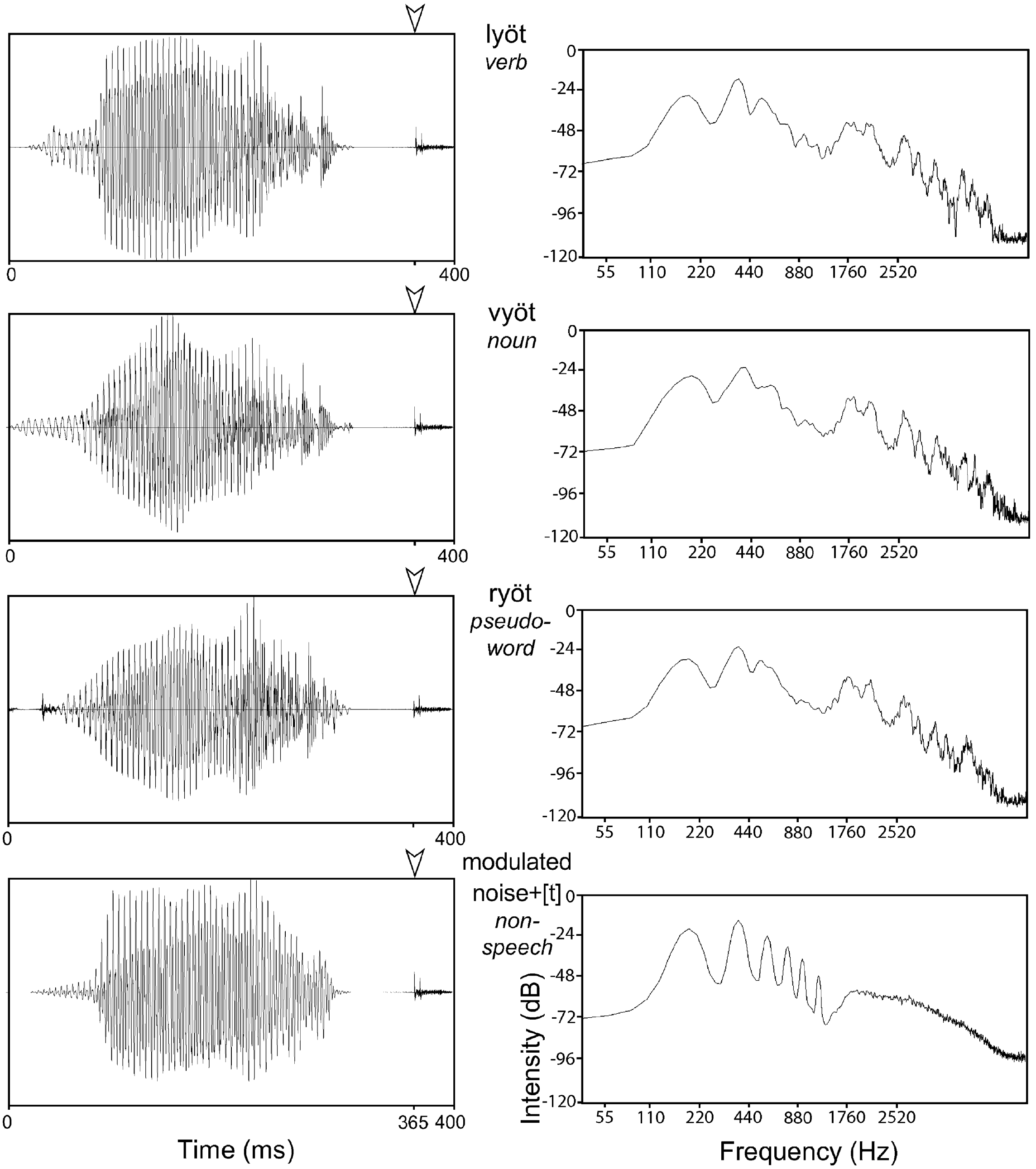

Fig. 1. The waveforms (left) and frequency component (FFT) analysis (right) of deviant acoustic stimuli used in the four experimental conditions: verb, noun, pseudoword, and non-speech complex sound. All stimuli were maximally matched for their acoustic properties. The standard and deviant stimuli in each condition are identical up to the divergence point at their end when the onset of final [t] takes place (marked with white arrowheads) in the deviant stimuli. This standard-deviant contrast is identical in all conditions, whereas the context in which it is presented varies (cf. Table 1).

has its limitations, because there are rapidly changing acoustic patterns that are not native speech sounds and that fail to elicit significantly lateralized responses (Best and Avery, 1999; Shtyrov et al., 2000b) and, vice versa, there are acoustically simple communication signals that do produce laterality (Gandour et al., 2000, 2003; Hsieh et al., 2000; Kujala et al., 2003; Papcun et al., 1974).

A major competing view, which we here call the phonological laterality theory, claims that non-speech and speech sounds are processed independently of each other and that there exists a specialized speech-processing module in the cortex. More specifically, it is argued that articulatory gestures are stored in the cortex and that their memory traces, which are thought to link sounds to corresponding articulation patterns, are preferentially treated by a putative dedicated speech module (e.g., Liberman and Whalen, 2000; Whalen and Liberman, 1987). If such a specialized mechanism indeed exists, it should be found in the perisylvian cortex of the left hemisphere (Braitenberg and Pulvermüller, 1992; Pulvermüller, 1999). This theory explains a number of psychoacoustic and psycholinguistic phenomena, among which the following is of interest here: short acoustic bursts perceived as stop consonants (e.g., [t]) when being a part of a spoken syllable, lose any resemblance with speech if presented in isolation or in conjunction with non-language sound (Liberman and Mattingly, 1988). This approach does provide a framework for explaining the speech processing in the brain, but similarly to the acoustic approach cannot fully account for the entire range of experimental data. For instance, it cannot explain differential laterality for phonemes such as reduced (or even absent) laterality in response to vowels as compared with stop consonants as revealed, e.g., by dichotic listening (Shankweiler and Studdert-Kennedy, 1967, 1975; Spellacy and Blumstein, 1970; Studdert-Kennedy and Shankweiler, 1970; Weiss and House, 1973).

Here, we set out to test the two main views on laterality by probing the brain response to the same acoustic event, a rapidly changing plosive sound, presented in different contexts. In one case, it appeared after a non-speech noise-like sound with spectro-temporal characteristics similar to a spoken syllable. In a different context, it was presented after a spoken syllable that did not make sense and did not form a meaningful language unit together with the final plosion. However, in this case, such plosion is perceived as an instance of the phoneme [t] in a meaningless pseudoword never encountered before. The acoustic theory of laterality would thus predict lateralized brain responses both in non-phonetic context and in meaningless syllable context, whereas the phonological theory would only predict laterality in the latter. In addition, we presented the same sound at the end of words where it is perceived as the phoneme [t] and also carries grammatical information.[1] We hypothesized that both main theories of cortical laterality might be incorrect and that reliable cortical laterality might only be elicited by a sound if it is presented in the context of previously encountered larger language units, namely meaningful words. Laterality might then be triggered by the existence of word-related neuronal assemblies (long-term memory traces) frequently activated in perception and production of such words. To asses activation of these memory traces, we recorded mismatch negativity (MMN), an automatic auditory change-detection response and an index of experience-dependent memory traces in the human brain (Kraus et al., 1995; Näätänen, 2001; Näätänen and Winkler, 1999; Picton et al., 2000). The MMN is a brain response automatically elicited by rare (deviant) stimuli occasionally presented in a sequence of frequent (standard) stimuli. It can be elicited in the absence of the subject's attention (Näätänen and Alho, 1995) and, furthermore, MMN responses to speech sounds were suggested not to be substantially affected by the presence or absence of attention to the individual stimuli (Alho et al., 1998). Recently, a number of studies demonstrated a selective left lateralized increase in the magnitude of mismatch negativity for native-language sounds including phonemes, syllables, and words as compared with other acoustically similar sounds (Alho et al., 1998; Näätänen, 2001; Näätänen et al., 1997; Pulvermüller et al., 2001b; Shtyrov et al., 1998, 2000b). This led to suggestions that the MMN may serve as a neurophysiological indicator of long-term memory traces for language elements.

Materials and methods

Subjects

Sixteen healthy right-handed (handedness tested according to Oldfield, 1971; no left-handed family-members) native Finnish speakers (age 21–39, 6 males) with normal hearing and no record of neurological diseases were presented with four different sets of acoustic stimuli in four different experimental conditions while their MEG was recorded.

Stimuli

The experimental stimulus set consisted of a total of eight items presented in four experimental conditions (see Table 1 for details). In two of the conditions, spoken Finnish words were used: a verb lyöt (2nd person singular for lyödä, Eng. hit) and a noun vyöt (plural nominative for vyö, Eng. belt) were presented as rare random deviant stimuli among frequent standard ones. The latter were the respective base forms lyö (stem/singular imperative of the same verb) and vyö (stem/singular nominative of the same noun). In the third condition, an acoustically similar pseudoword ryöt (meaningless but phonotactically regular) was presented as a deviant stimulus against the standard stimulus ryö (also pseudoword). Finally, in the fourth condition, two non-linguistic stimuli acoustically similar to the above words and pseudowords were contrasted. Below we describe the procedure of stimulus preparation in more detail.

We digitally recorded (sampling rate 44.1 kHz) multiple repetitions of syllables lyö, vyö, ryö and additionally one more word–työt–uttered by a female native speaker of Finnish and with great care selected a combination of the four items whose vowels matched in their fundamental frequency (F0) as well as sound energy and overall duration. The matched three syllables were used as such as the standard stimuli. To produce the deviant stimuli (lyöt, vyöt, and ryöt) with minimal acoustic differences between the conditions (which is highly important in such experiments), we used identical recording of the final phoneme [t] in each deviant sound. To achieve this, one needs to use cross-splicing, i.e., combining sounds from different recordings to form a single item. To avoid differential effects of co-articulatory cues (which would arise should the final plosion be drawn from one of the actual stimuli and copied to the other two), we selected to take it from a similar word not used as such in the experiment. The word-final sound [t] was therefore cross-spliced from the recording of työt to vyö, lyö, and ryö. The pause of about 60 ms preceding the final stop consonants in this type of Finnish monosyllabic stimuli (Fig. 1) makes such stops an ideal target for cross-splicing, and we were thus able to smoothly combine the phonemes producing naturally

Table 1
Auditory Finnish language stimuli used in the four experimental sessions

	Verb context	Noun context	Pseudoword context	Non-speech context
Deviant	**lyöt**	**vyöt**	**ryöt**	**[*complex sound*] + [t]**
	verb	*noun*	*pseudoword*	*non-speech*
Standard	lyö	vyö	ryö	[*complex sound*]
	verb	*noun*	*pseudoword*	*non-speech*
Control Standard	**lyöt**	**vyöt**	**ryöt**	**[*complex sound*] + [t]**
			same as deviants	

All stimuli were maximally matched for their acoustic properties (cf. Fig. 1). The standard-deviant contrast is identical in all conditions, whereas the context in which it is presented varies. The MMN was calculated as a difference between responses to the same sounds presented as deviant and standard stimuli (Deviant − Control Standard recordings, in bold), which allowed us to further disentangle purely acoustic effects on the MMN from those of context.

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[1] Finnish-language stimuli were used (see Materials and methods): [t] at the end of a noun in Finnish indicates plural nominative/accusative, and at the end of a verb signifies 2nd person singular.

sounding stimuli with precisely controlled acoustic features. The sounds were normalized to have the same loudness by matching their root-mean-square (RMS) power. To ensure even smaller acoustic differences between the stimuli, RMS power was separately normalized for the onsets and the final stops of the stimuli. Such meticulous procedure of stimulus preparation is essential for auditory experiments, since the auditory system's evoked responses are highly sensitive to acoustic differences between the stimuli; this is especially true for the mismatch negativity responses which are sensitive to standard-deviant contrasts. All deviant stimuli were 400 ms and the standards ones were 310 ms in duration. The standard and deviant stimuli diverged acoustically for the first time at 365 ms after their onset which was when the final plosion in the deviants started (Fig. 1). This physical divergence point is thus the earliest point in time after which differences between standards and deviants can be perceived. This point is therefore the onset of perceptual contrast and is used as a zero time reference in the current study.

The non-speech set of stimuli was created with a goal to produce non-language complex sounds approximating the acoustic complexity of the words and pseudowords in the other three sets as well as their deviant-standard difference. For this purpose, a complex sound (Fig. 1, bottom) 310 ms in duration was created by generating acoustic noise with frequencies selectively increased in the bands corresponding to the first six formants of the language items. This was done by applying fast Fourier transform (FFT) filter whose profile was derived from the frequency decomposition of the other stimuli. To further enhance the similarity with the language items and to mimic voicing effect, a similar combination of six sine-wave tones was produced and combined with the filtered noise. The length and envelope of this non-speech fragment were based on those of the syllables in the other sets. This fragment was presented as such as a frequent repeated standard stimulus in the non-speech condition. For producing its deviant counterpart, we cross-spliced it with the same plosion which was perceived as the final [t] in the spoken stimuli using the procedure identical to that applied to the word and pseudoword deviants. Although this short sound was derived from a real-speech recording, in the non-speech context it could not be identified as a phoneme by subjects who were asked to detect any speech or language sounds in these artificial items. The signal power of the non-speech stimuli was normalized to match that of the other stimuli using the procedure identical to the one described above. For the analysis and preparation of the stimuli, we used the Cool Edit 2000 program (Syntrillium Software Corp., AZ, USA).

This way, we created 4 pairs of standard and deviant stimuli with precisely controlled acoustic features and highly similar to each other (Fig. 1 and Table 1). Most importantly, the standard-deviant acoustic-phonetic contrast, the critical variable determining acoustically-related MMN (Näätänen and Alho, 1997), was identical in all conditions (absence vs. presence of the final [t]), thus controlling for purely acoustic, phonetic, and phonological effects on mismatch responses. Crucially, however, the MMN responses elicited by this identical acoustic contrast were generated in four distinct contexts: that of meaningful verb, noun, meaningless pseudoword, and a non-linguistic item. The four conditions are below referred to as Verb Context, Noun Context, Pseudoword Context, and Non-speech Context.

To further control for any possible acoustical effects on the MMN responses, we also obtained brain responses to the four [t]-ending items as frequently repeated standard stimuli; we then compared responses to the same sounds presented as rare unexpected deviants and frequent standards to produce the MMN.

Acoustic stimulation

In Verb- and Noun-Context conditions, the inflected forms lyöt and vyöt were presented among their respective base forms lyö and vyö. In Pseudoword condition, the pseudoword ryöt was contrasted with pseudoword ryö. In Non-speech condition, the complex non-speech sound served as the standard, whereas its [t]-ending form was the deviant. The inter-stimulus interval (onset-to-onset, SOA) was 900 ms. The stimuli were presented binaurally at 50 dB above individual hearing threshold via earpieces connected to a STIM set-up (Neuroscan Labs, Sterling, VA). In each condition, the deviant stimulus was presented with 14.2% probability among the repetitive standard stimuli: pseudo-random stimulus sequences were created so that there were always at least two standard stimuli between any two deviants.

In the end of each block, the otherwise deviant stimuli were also presented repeatedly at least 300 times to collect brain responses to them as standard sounds. These additional conditions were performed in order to obtain responses to the acoustic items as both deviant and standard stimuli, which allowed us to disentangle purely acoustic effects (which could still arise due to basic sound differences between the stimuli) from the effects of context. The order of the four experimental conditions was counter-balanced across the subjects.

Magnetoencephalographic recording

The subjects were seated in magnetically shielded room (Euroshield Ltd., Eura, Finland) and instructed to pay no attention to the auditory stimulation and to concentrate on watching self-selected silent videofilm. The evoked magnetic fields of the subjects' brain were recorded (passband 0.03–200 Hz, sampling rate 600 Hz) with a whole-head 306-channel MEG set-up (Elekta Neuromag, Helsinki) during the auditory stimulation (Ahonen et al., 1993). The recordings started 100 ms before stimulus onset and ended 900 ms thereafter. The responses were on-line averaged separately for all types of stimuli in each condition. Epochs with voltage variation exceeding 150 μV at either of two bipolar eye-movement electrodes or with field-intensity variation exceeding 3000 fT/cm at any MEG channel were excluded from averaging. The recordings for each condition contained the minimum of 150 accepted responses to deviant stimuli and at least 300 for the same items frequently repeated as standards at the end of the block.

Data processing

The averaged responses were filtered off-line (passband 1–20 Hz) and linear detrending was applied on the entire epoch. The silent period of 50 ms before the divergence point (the onset on final [t]) was used as the baseline. The magnetic MMN (MMNm) in each condition was obtained by subtracting the averaged response to the same sound presented as standard stimuli from that to the deviant ones. The responses were then separately evaluated for each subject's left and right cerebral hemisphere for all experimental conditions. To this end, a quadruplet of gradiometer channels where the responses were maximal was identified in each hemisphere. To quantify the event-related magnetic fields, vector sums of recordings in gradiometers located over temporal lobes in each hemisphere were computed and the resulting vector's absolute magnitude was used in further analysis. Its amplitude maximum was located separately for each subject, hemisphere, and condition. Average amplitude in the 40-ms window around each maximum was then computed. These area-mean amplitudes were compared between the recording sites/hemispheres and conditions. The range of latencies accepted for the MMNm responses was 90–300 ms after the divergence point. Matlab 6.5 programming environment (MathWorks, Boston, MA) was used for the procedures described above.

To quantify the hemispheric asymmetry of brain responses, we calculated a laterality coefficient Q similar to that used in earlier handedness, REA, and MEG studies (Hugdahl, 1988; Oldfield, 1971; Repp, 1977; Shtyrov et al., 2000a):

$$Q = \frac{A_l - A_r}{A_l + A_r} \times 100\%$$

where A_l and A_r are response magnitudes in the left and right hemispheres, respectively. Such laterality coefficients also provide a benefit of scaling the responses in each condition, thus removing a possible influence of overall differences in absolute magnitudes on the statistical analysis.

To further assess the responses and estimate locations of their activity generators, additional source analysis was performed. Fifty-four gradiometer channels on each side of the magnetometer helmet were used for assessing cortical responses in the left and right cerebral hemispheres. By means of sequential single-dipole fitting software (Elekta Neuromag), the generator sources (equivalent current dipoles, ECD) of the MMNm were estimated (Ilmoniemi, 1993); only dipole models explaining more than 65% of the field gradients were accepted. Finally, to visualize the ECDs and obtain the estimate of the activity origin in the brain, the grand-average dipole solutions were projected onto the standardized brain's magnetic-resonance image (MRI) using BESA 2000 software (MEGIS Software GmbH, Munich).

Since the magnitude of event-related fields (ERFs) registered in MEG is influenced not only by the source strength but also by the distance between the source and the sensor, the head position inside the helmet was also controlled. The head origin coordinates were obtained for each subject/session and then analyzed statistically to control for a possible influence of different head positions in different recording blocks.

The statistical analysis of all data was carried out with the analysis of variance (ANOVA) test. Stimulus types and recording sites (including left vs. right cerebral hemispheres) were used as within-subject factors. F tests were used in further Planned Comparisons analysis.

Results

Event-related fields were successfully recorded and MMNm responses were calculated for all four conditions in both hemispheres. However, the responses differed between the conditions and the two hemispheres (Figs. 2–5).

Statistical analysis of response amplitudes indicated that in both word (i.e., Verb- and Noun-Context) conditions, the mismatch negativity in the left hemisphere was significantly larger than in the right one ($F(1,15) = 6.0$, $P < 0.03$). However, no significant differences between the hemispheres could be found either in the Pseudoword Context ($P = 0.3$) or in the Non-speech Context ($P = 0.7$). These differences in laterality of MMNm responses between the conditions were further substantiated in a significant Stimulus Type × Hemisphere interaction comparing the meaningful words and meaningless stimuli ($F(1,15) = 4.7$; $P < 0.05$). The above effects could only be seen for the MMNm responses; when the same stimuli were presented as repeated standards, no laterality differences between ERFs to different stimuli could be found (Fig. 4).

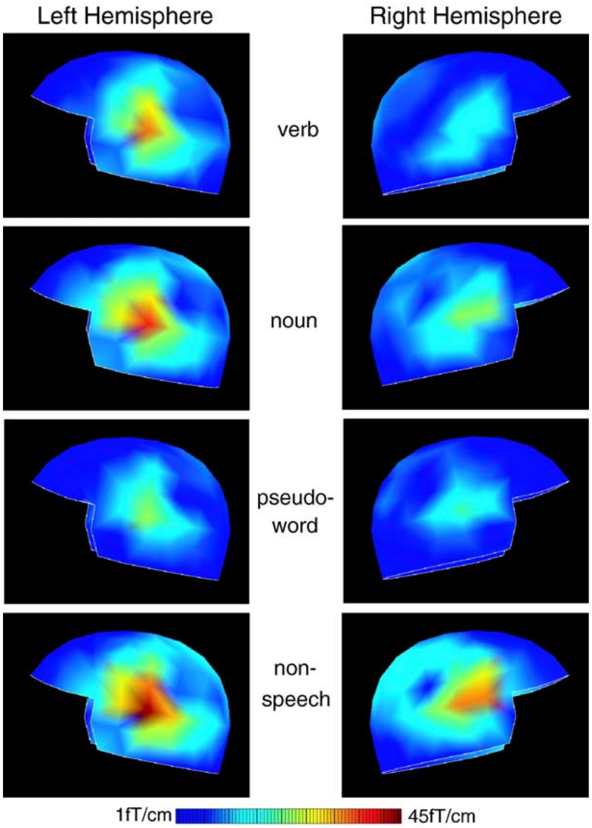

Fig. 2. Magnetic field gradient intensity maps of MMNm responses elicited by the four types of stimuli: left and right lateral views. Maximum response magnitudes could be found over the temporal lobes. Notice the larger left–right difference in the word conditions, reduced laterality for the pseudoword and non-speech stimuli, and larger responses for the words than the pseudoword.

To further analyze the results and to remove a possible contribution of different MMNm magnitudes, analysis of laterality coefficients was performed. This also confirmed larger left hemisphere's dominance in word-evoked MMNm activity (mean Q being 8% for Noun, 14% for Verb, 3% for Pseudoword, and 0% for Non-speech contexts). The difference between laterality coefficients was significant for comparison between the word items and the pseudoword ($F(1,15) = 5.6$; $P < 0.04$) as well as for comparison between both word conditions and Non-speech ($F(1,15) = 6.1$; $P < 0.03$).

Table 2
ECD magnitudes in the left and right hemispheres (dipole moments and respective standard errors of mean, nAm)

	Verb	Noun	Pseudoword	Non-speech
Left	24 (2)	22 (3)	16 (3)	23 (4)
Right	12 (2)	11 (2)	10 (2)	18 (4)

A more specific analysis of responses to the three spoken items demonstrated a significant main effect of stimulus type ($F(2,30) = 6.9$; $P < 0.01$), which, as revealed by planned comparison tests, was due to a larger response amplitude to both words than to the pseudoword ($F(1,15) = 6.5$; $P < 0.03$, see (Figs. 2, 3, and 5)). This effect of enhanced MMN amplitude to meaningful words as compared with acoustically similar pseudowords confirmed earlier findings (Korpilahti et al., 2001; Pettigrew et al., 2004a; Pulvermüller et al., 2001b; Shtyrov and Pulvermüller, 2002b; Sittiprapaporn et al., 2003) and was most pronounced for the recordings over the left cerebral hemisphere ($F(1,15) = 10.5$; $P < 0.01$), while not reaching significance for the right one ($P = 0.2$).

Analysis of equivalent current dipole moments indicated a similar diverging pattern of response laterality and magnitude (Table 2). The ECD model analysis suggested no significant differences in location of cortical generators of the four MMNs. All dipole sources were estimated to be in the posterior part of the superior temporal gyri (in the vicinity of Heschl's gyrus) in both cerebral hemispheres (Fig. 6).

Mean peak latencies of the MMNm responses and respective standard errors of mean were 148 (8) ms in Verb condition, 138 (7) ms in Noun condition, 155 (15) ms for Pseudoword, and 138 (7) ms for Non-speech condition. Response latencies did not significantly differ between the conditions or hemispheres.

The analysis of head origin positions within the MEG sensor array did not show any significant differences between the experimental blocks ($P > 0.64$), thus implying that between-condition variations in the head position could not possibly account for the reported results. Furthermore, in both blocks with word stimuli, the average head position was slightly closer (by ~0.1 mm) to the right than in pseudoword and non-speech conditions. Therefore, if such negligible and non-significant difference in head position could have possibly biased the results, this bias would have been against the pattern reported here (stronger left than right activation for word items), thus implying a certain degree of robustness of the reported effects.

Discussion

When the same rapidly changing short sound was presented in non-speech and language contexts to right-handed monolingual subjects without left handed family members, left lateralized mismatch negativity responses were seen only in word context. No significant laterality was observed when the stimulus followed non-phonetic sound spectrally and temporally similar to the spoken syllables, thus failing to support the acoustic laterality theory according to which all fast changing spectrally rich sounds should lateralize. Nor did the experimental sound elicit lateralized MMNs when presented in the context of a meaningless pseudoword where it is perceived as a prototypical example of the consonant [t]. This fails to support the second main theory attributing laterality to phonological processes (phonological laterality theory). Significant laterality of the MMN was only seen when the plosion was presented in word context, thus supporting the view that cortical laterality in language processing is critically dependent on the acquisition of cortical memory networks for spoken words. We will try to assess the results in more detail below.

The acoustic contrast between the standard and deviant stimuli is the primary feature related to MMN elicitation and its magnitude

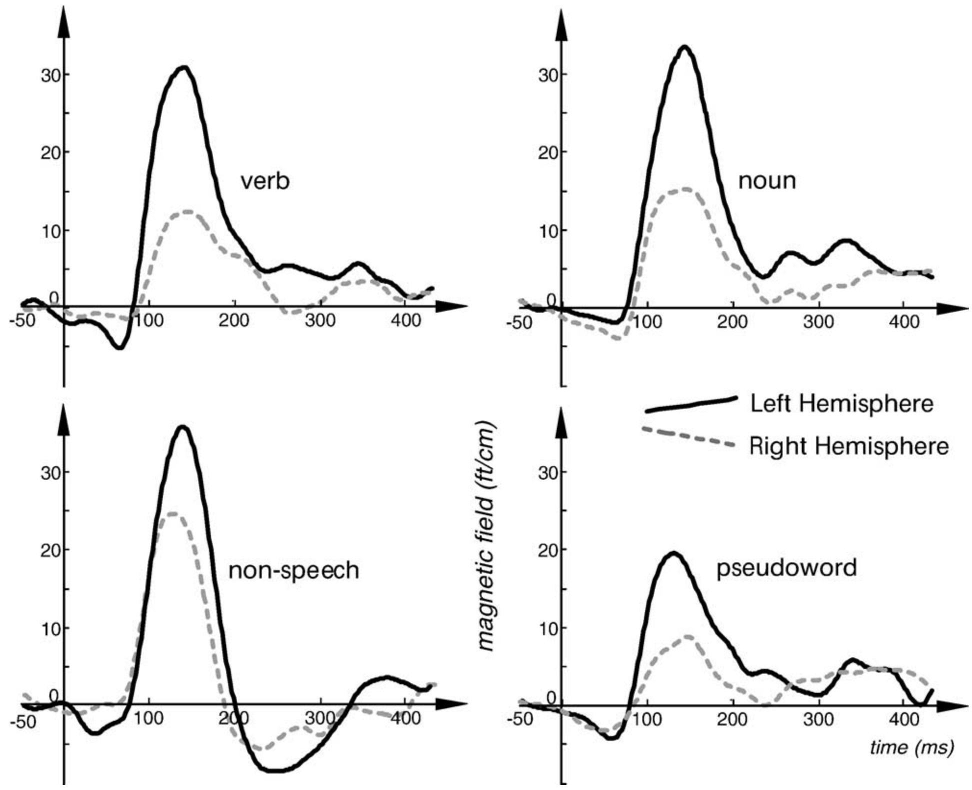

Fig. 3. MMNm responses elicited by the four types of stimuli in the left and right cerebral hemispheres (grand-average MEG difference waveforms). Gradiometers with the maximum response amplitudes located over the left and right temporal cortices are shown. Note the larger left–right difference for the word items, reduced laterality in pseudoword and non-speech items, and larger response for words than the pseudoword (in the left hemisphere in particular).

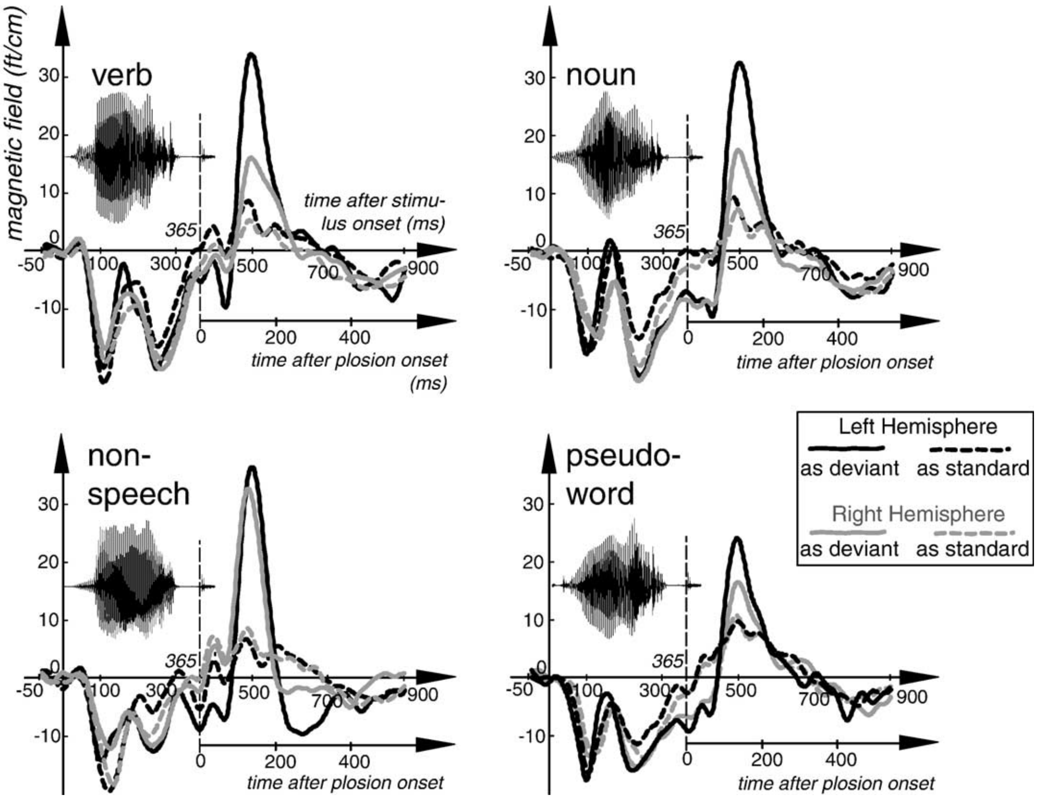

Fig. 4. Magnetic-evoked responses elicited by the four types of stimuli in the left and right cerebral hemispheres (grand-average MEG waveforms). Standard and deviant responses elicited by the physically identical items presented in different positions are shown (overlaid by acoustic stimulus waveforms for reference). Epochs start from pre-stimulus interval; baseline correction here done for −50 to 0 ms before the stimulus onset. Note the larger left–right difference for the word deviant items, reduced laterality in pseudoword and non-speech deviant items, larger response for words than the pseudoword deviants, and the absence of such effects for the same sounds presented as standard stimuli.

(Näätänen and Alho, 1997). This was kept constant across conditions. Furthermore, to reduce any effects of the acoustical differences between the stimuli, they were matched for their sound energy, duration, and other spectro-temporal parameters. The MMNm was computed using standard and deviant responses to acoustically identical items, thus further reducing any differential influence of stimulus features on the responses. It therefore seems most reasonable to suggest that it was the differential context of the four stimulus conditions that played the crucial role in generating diverging patterns of hemispheric asymmetry of MMNm amplitudes.

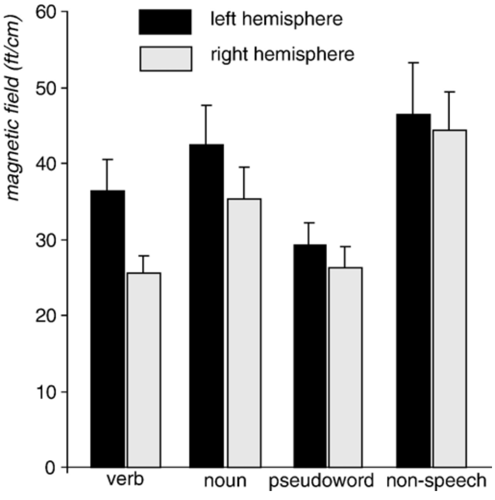

Fig. 5. Mean amplitudes and standard errors of mean of MMNm responses elicited by the four types of stimuli in the left and right temporal lobes. Note the larger left–right difference in both word conditions, reduced laterality for pseudoword and non-speech items, and larger response for words than for the pseudoword.

Words representing two parts-of-speech (verb and noun) produced clear left hemispheric dominance, which is in agreement with the known facts regarding cerebral asymmetry for language. The pseudoword was phonologically and phonotactically legal in the Finnish language; in fact, experiment participants, when asked to assess the stimuli after the MEG recording, made a comment that it "could have been" a Finnish word. In the same time, the non-speech stimuli (with or without the final [t]) generated no phonemic perception. However, in the degree of hemispheric laterality, the pseudoword was much closer to that of the non-speech stimulus than that of the words. Since the experimental design rules out any acoustic differences as possible reasons for this discrepancy, it seems that other factors should have contributed to this dissociation: namely, for both experimental words, the brain must have pre-existing memory traces formed in the previous experience of speech perception and production; however, no such representations could be present for the pseudoword and the non-linguistic item due to their unfamiliarity. We therefore suggest that it is the activation of these memory networks for the known items that produced larger left–right asymmetry for the words than for the other two stimuli. The issue of cerebral laterality of speech thus appears to be linked to the mechanisms underlying the processes of formation of such memory traces.

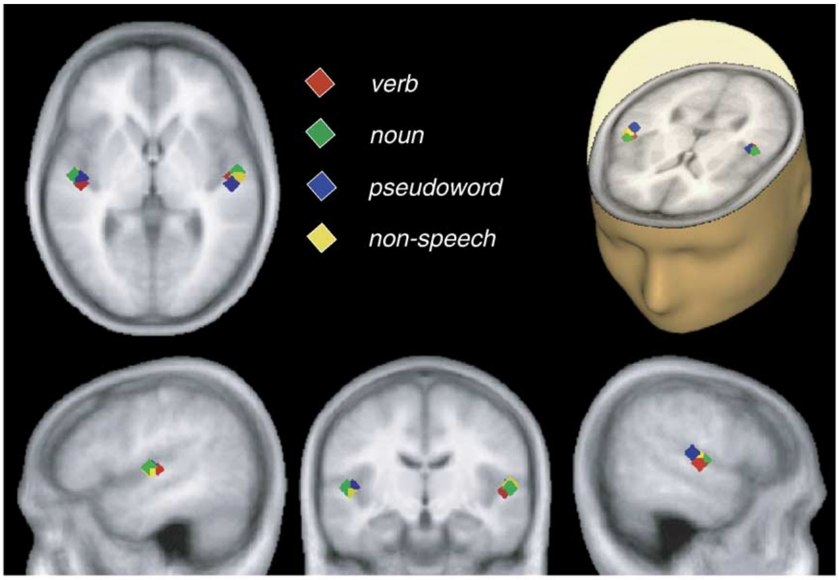

Fig. 6. Grand-average locations of MMNm source generators for the four stimuli in the left and right temporal lobes: magnetic resonance images superimposed with MEG dipole models. Cortical generators of the four MMNs did not significantly differ between themselves and were estimated to be in posterior part of the superior temporal gyri in both cerebral hemispheres.

Crucially, as the critical sound for eliciting the MMNm, we used a plosive stop consonant. Stop consonants have always been characterized by their rapid onset and offset patterns and rich spectral characteristics. The rapidity aspect of speech and of its stop consonants in particular was often suggested as a reason for left hemisphere's dominance in speech perception based on the proposal that this hemisphere has an advantage in processing any rapid spectrally complex sound (Fitch et al., 1997; Tallal et al., 1993; Zatorre and Belin, 2001). Here, we demonstrate that this putative feature is not sufficient for causing the full degree of laterality during language processing: fully-fledged and statistically significant left hemispheric dominance was seen only for the stimuli familiar to the central nervous system, which had presumably developed memory networks for them. The same identical rapid complex sound did not produce significant laterality when presented in the context of meaningless items; this was regardless of their classification as being speech/language or not. They were obviously processed more bilaterally than the meaningful native language elements. Similarly, the reduced laterality for the pseudoword stimulus implies that even if the speech-specific mechanisms did exist in the left hemisphere, the presentation of a native-language phoneme is still not sufficient for their activation. This rules out an explanation of the present data using the phonological approach to laterality (Liberman and Whalen, 2000).

We realize that the absence of a significant asymmetry for non-speech and pseudoword contexts is a null result which per se cannot unequivocally reject the tested theories. However, the strong result perpetuated by the present study is the significant interaction of the stimulus type and laterality factors, thus proving that word contexts either produce laterality, or, if it were present in the first place, greatly increase it. The presence of this interaction cannot be explained by and therefore falsifies both acoustic and phonological theories of speech laterality. The fact that a larger meaningful element of communication is regularly used in spoken language and has its established memory trace or network in the cortex seems to be a precondition for this laterality enhancement to occur. Given this observation, there are now several possibilities to further investigate the linguistic nature of the observed laterality, among which we wish to highlight the following three:

(1) The linguistic nature of the word final phoneme stimulus could be relevant. The [t] in our word stimuli was always an inflectional affix conveying grammatical information about the verb (person) or noun (number/case) in question. Inflectional affixes and grammatical function words have previously been shown to elicit stronger laterality than other lexical types (Pulvermüller et al., 1995; Shtyrov and Pulvermüller, 2002a). In this case, the laterality enhancement could reflect grammatical information attached to a phoneme, which would accordingly be absent in pseudoword context.

(2) As a more general possibility, all known meaningful words could be capable of eliciting the laterality enhancement, not just inflectional affixes.

(3) Finally, it could be that the laterality enhancement is specific to all complex acoustic patterns that the individual is familiar with and has learnt to articulate. In this case, at the heart of the laterality enhancement could be sensory-motor learning, i.e., the build-up of a memory trace for frequently produced sounds. This would suggest, for example, that also CV syllables frequently used already by infants during babbling, e.g., [ba], [ta], and [ka], should elicit significantly lateralized MMNs indistinguishable from those to words. Although some previous results suggest this possibility (Shtyrov et al., 2000a,b), we emphasize the need for future research into the MMN laterality enhancement to words and other familiar acoustic stimuli.

Importantly, in the current data, the identical acoustic contrast produced larger MMNm when it was elicited by meaningful words as opposed to acoustically matched, phonologically similar, and phonotactically legal pseudoword. This confirms earlier EEG and MEG findings (Korpilahti et al., 2001; Pettigrew et al., 2004a; Pulvermüller et al., 2001a, 2004; Shtyrov and Pulvermüller, 2002b; Sittiprapaporn et al., 2003) that identical acoustic contrasts produce stronger MMN in response to word deviant stimuli than pseudoword ones. This enhancement is seen here as most profound in the left hemisphere but bilateral or even right hemispheric MMN enhancement has also been reported which may be due to particular (e.g., semantic) properties of the word stimuli involved (Kujala et al., 2002; Pulvermüller et al., 2004). Together with previous studies, the current results further support the hypothesis that MMN is sensitive to long-term memory traces–or distributed memory networks–for language elements.[2] Formation and maintenance of memory traces are related to a number of different neuronal processes, many of which are poorly understood, especially in cases of human-specific cognitive functions such as language. The evidence of cellular-level mechanisms of cortical memory traces, novelty detection, and MMN generation has only recently started to emerge (Nelken et al., 2003; Ranganath and Rainer, 2003; Ulanovsky et al., 2003). At any rate, such memory traces should incorporate multiple feedforward and feedback connections between participating neurons/neuronal groups (Pulvermüller, 1999, 2001). We hypothesize that it is the activation within these strongly connected networks that accounts for the increase of magnitude of the event-related response in meaningful word context, as compared with pseudowords context. The present result provides impressive evidence for the magnitude of this cognitively related neurophysiological difference (up to >10 fT/cm).

The reported effects of laterality and lexical enhancement were present for the MMNm responses elicited by rare deviants, but could not be found for the same sounds presented as frequent standards. Although in our view there is no compelling reason to refute lexical enhancement for the standard stimuli which serve as the basis of deviance detection by determining the context of sound sequence (Sussman et al., 2003), such an enhancement is rarely seen (and it is difficult to exclude that it is related to the physical rather than linguistic properties of eliciting stimuli, see e.g., Jacobsen et al., 2004). The exact reason for the absence of such effects in standard responses (including N1) cannot be confirmed at this stage and remains to be investigated. On the other hand, even the current design cannot completely exclude a possibility of partial N1 contribution to the differential responses to the deviants; this, however, does not change the main result and the conclusions regarding differential ERF laterality. An ongoing discussion in the literature as to what extent MMN and N1 reflect activity of the same or different neural structures (see e.g., Jääskeläinen et al., 2004) will hopefully shed more light on the issue as new experimental evidence gradually appears.

Unlike the pseudoword, the meaningless non-speech stimulus elicited a pronounced MMNm in the current study similar in magnitude to that to words (Fig. 3). This may be explained by a different mechanism being triggered by the non-linguistic perception, which is more salient or more attention-attracting than the speech sounds. Whereas linguistic spoken stimuli are putatively compared against pre-existing long-term memory traces which are activated in case they match the input, non-language items may be processed via a different route. In the latter case, the deviant stimuli are compared by the auditory system with short-term memory traces created for the standards in the course of experimental session, and in case of mismatch, a classical change-detection-related MMN is generated. Indeed, it has been observed that non-speech acoustic stimuli usually elicit more pronounced MMNs than those related to language (e.g., Ikeda et al., 2002; Wunderlich and Cone-Wesson, 2001). A further possibility is that the non-speech complex sounds were more novel and unusual for the volunteers than the spoken stimuli and therefore could possibly attract more involuntary attention which in turn increased the response magnitude (Szymanski et al., 1999). As another alternative, it was the stimulus-final plosion (stop consonant) that could not be expected to occur in non-speech context and therefore elicited a more pronounced response. The latter two suggestions are supported by a P3-like deflection which can be seen as following the MMNm in the non-speech condition but not in the other ones (Fig. 3). P3 is known to reflect attention-related processes including triggering involuntary attention to acoustic novelty and change (Donchin, 1981; Escera et al., 1998).[3]

We also wish to remark on the possible implications of the present results for psycholinguistic and neuropsychological theories. It has been stated that affixes of nouns and verbs may be processed by distinct sets of neural populations in different cortical areas (Shapiro and Caramazza, 2003). On the basis of the present results, we cannot support this claim: we found no differences in current source locations between the stimulation conditions. Admittedly, a minimal difference (on the millimeter range) in location of cortical generators for noun and verb suffixes would probably escape the present analysis procedures and therefore cannot be excluded. It has also been suggested that an inflectional suffix attached to a pseudoword (ryöt in the current study, a comparable English example could be a "pseudo-past" form such as "wugged") can, if it is in accordance with phonotactic and morphological rules of the language, be processed as an inflectional suffix even though its context is not meaningful (Tyler et al., 2002). This approach would predict that the neurophysiological signature of inflectional affixes, clear left laterality with sources in or close to perisylvian regions (Pulvermüller et al., 1995, 2001a; Shtyrov and Pulvermüller, 2002a), would be present equally in word and pseudoword context, a prediction not confirmed by the data. The reduced amplitude and absent laterality of MMNm to the pseudoword final [t] suggest that a lexical context is required for the automatic recognition of this element as an inflectional suffix of Finnish.

Finally, the present study has some methodological implications. First, we applied the traditional oddball paradigm to studying fine-grain properties of neural sound processing. For this, the paradigm was modified in a way which provided maximally controlled physical sound features, most notably by using identical acoustic contrasts in all conditions, whereas the stimulation context was systematically varied. This seems to be a fruitful approach. Secondly, the studied contrasts were placed in the stimulus-final positions. One may argue that the preceding acoustic information still differs between conditions; however, this is controlled by subtracting the standard response from the deviant one to calculate MMNm, thereby canceling out the identical contribution of the pre-divergence acoustic input. To further reduce any differential

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[2] Whereas a minority of studies failed to find linguistic effects on MMN (Jacobsen et al., 2004; Wunderlich and Cone-Wesson, 2001), this is most likely due to methodological differences, most notably stimulus construction issues (see also Materials and methods for discussion of acoustic stimulus properties in language experiments).

[3] The other possible implication of the presence of such a deflection in the non-speech condition, whereas it was absent for all natural spoken stimuli equally, is that there was probably no differential attention allocated to the three spoken items.

influence of the preceding acoustic information, we applied baseline correction before the onset of the critical sound (cf. Figs. 3 and 4). The strategy of placing the baseline within the stimulus rather than before it can be risky in general, but in the current study, the stimuli were constructed in a manner which provided a silent baseline interval before the onset of the final plosion: a silent pause which precedes word-final stop consonants in Finnish allows for such clean baseline interval (see Fig. 1). Further, we used a well-defined acoustic contrast (plosion vs. silence) to generate a pronounced MMNm with high signal-to-noise ratio, but for calculating it, responses to the same sounds in frequent standard positions were recorded and subtracted from the deviant ones, thereby controlling for the obligatory responses (e.g., N1) to the same plosion. This approach resulted in robust MMNm signals unlike the low-amplitude MMNs usually reported for speech sounds (cf. Shtyrov et al., 2000b). In sum, such carefully constructed MMN paradigm using meticulously prepared stimuli appears to be a valuable tool for studying spatio-temporal patterns of language-related activity in the human brain (for review, see Pettigrew et al., 2004b).

The effects reported in the current study were found in a non-attend paradigm using the MMN response traditionally seen as an index of automatic attention-independent auditory processing (Näätänen, 1995; Näätänen and Winkler, 1999). The differential patterns of responses were observed already at ~100–150 ms after the relevant acoustic information became available in the auditory input. These results suggest that the language-specific processing of auditory information commences rather early in time and is largely independent of the focussed attention.

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