

Research report

Dynamic sensory updating in the auditory system

Elyse Sussman^{a,*}, István Winkler^{b,c}

^aDepartment of Otolaryngology, Albert Einstein College of Medicine, 1410 Pelham Parkway S, Bronx, New York, NY 10461, USA

^bInstitute of Psychology, Hungarian Academy of Sciences, H-1394, Budapest P.O.B. 398, Szondi u. 83/85, Hungary

^cCognitive Brain Research Unit, Department of Psychology, P.O. Box 13 (Meritullinkatu 1) FIN-00014 University of Helsinki, Helsinki, Finland

Accepted 6 June 2001

Abstract

Typically, in everyday situations, auditory input is constantly changing. Change is an important cue for the auditory system, which can signal the start of new sources of information or that some action may be required. Using an event-related brain potential that can be elicited whether or not attention is focused on the sounds (the mismatch negativity, MMN) we measured the time course of the effects of contextual changes on the brain's response to the same stimulus event. The onset or cessation of a sound in a stimulus block brought about context changes. The effect of the context was observed through changes in the MMN response to a deviant event that was present throughout the sound sequence. These results suggest the existence of a dynamic system of change detection, which updates its model of the sensory input on-line as the changes occur. © 2001 Elsevier Science B.V. All rights reserved.

Theme: Neural basis of behavior

Topic: Learning and memory: systems and functions

Keywords: Sensory updating; Auditory processing; Mismatch negativity; Context effect; Sensory learning

1. Introduction

The perception of a sound is often determined by the sounds that surround it, such that changes in the larger context may affect processing of the individual components. The ability of the auditory system to detect contextual changes (such as the onset or cessation of sounds within an ongoing sound sequence) thus plays an important role in auditory perception. In the current study we investigated the dynamics of context-change detection by determining the time course within which changes of the context affect the processing of individual sounds. The purpose was to examine how the neural representation of the auditory input accommodates to subtle but far-reaching changes in the acoustic signal.

Event-related potentials (ERPs), because they are time-locked to sensory events and have a high temporal resolution, allow us to study the time course of information processing in the human brain. The mismatch negativity

(MMN) ERP component ([10]; for recent reviews see [12,13]), a useful tool for studying auditory neural representations, is elicited by infrequent violations of acoustic regularities. It is generated mainly in or near primary auditory cortex¹ [1] and can be elicited whether or not the experimental participant focuses on the sounds. The simplest way to elicit MMN is to infrequently present sounds that differ (e.g. in frequency, intensity or duration) from a frequently repeating sound (this set-up is termed the auditory oddball paradigm). The cortical sound representations, extracted from the recent acoustic stimulation and maintained in auditory sensory memory, form the basis for the MMN-generating change detection process (for detailed discussions, see [9,11,12,15,16]). Incoming sounds are compared with the neural representations of the regularities present in the acoustic environment and those sounds that mismatch the representations elicit MMN.

*Corresponding author. Tel.: +1-718-430-3313; fax: +1-718-430-8821.

E-mail address: esussman@balrog.aecom.yu.edu (E. Sussman).

¹The location of the MMN generators in auditory cortex can account for the scalp topography of the waveform, which is maximally negative over the fronto-central regions of the scalp and invert in polarity at electrode sites located below the Sylvian fissure.

Therefore, the MMN, which typically peaks between 100 and 200 ms from the onset of acoustic change, provides a measure of the timing of early auditory sensory discrimination processes.

When two different deviations from the same repetitive standard occur successively within a <200 ms interval (a double deviant), only one MMN is elicited by them [4,17,19]. The two deviations are integrated into a single deviant event, irrespective of whether the physical deviations are carried by a single stimulus or two discrete stimuli. However, when double deviants were presented within a stimulus sequence that also contained single deviants (i.e. sounds that differ from the repetitive standard in one of the two ways of the double deviants), the double deviants elicited two discrete MMNs, which were separated in latency by the temporal distance of the successive deviations [Sussman and Winkler, unpublished data]. One possible explanation of this result is that when only double deviants are presented amidst the standard sounds, the second of the successive deviants does not provide new information about 'deviancy', because every time a deviant occurs the second one follows it. Thus the auditory system can preattentively extrapolate from the first deviant to the upcoming second deviant [9,20]. However, when the double deviants are mixed with single deviants in the sound sequence, the second successive deviant carries new information, which should be processed separately from the first deviant. In this case, the second deviant distinguishes the two types of deviants presented in the block. The presence or absence of single deviants in the sound sequence creates different contexts for the evaluation of the double deviants and, therefore, the double deviants are processed either as unitary events or as two successive events depending on in which context they occur.

In the current study, we exploited the effect of the single deviants on the response to double deviants in a paradigm that allowed us to examine the dynamics of contextual change, as might happen in more natural settings. We hypothesized that contextual changes (the emergence and disappearance of single deviants in a repetitive sound sequence) would affect processing of the double deviants, such that double deviants would elicit one or two MMNs time-locked to the contextual changes. Observing changes in the neural response to the double deviants as a function of the surrounding context would demonstrate the dynamics of updating the auditory sensory context.

2. Materials and methods

2.1. Subjects, stimuli and procedures

2.1.1. Subjects

Ten healthy adults (four males) ranging in age from 19 to 38 years with reportedly normal hearing participated in the experiment. All participants gave written informed

consent after the procedures of the study were explained to them. Subjects were paid for their participation.

2.1.2. Procedures

Two experimental sessions were conducted on separate days for each participant. Fifty stimulus blocks were recorded all together, 25 stimulus blocks per session. Each stimulus block consisted of three segments of 400 stimuli each (1200 stimuli all together), lasting 1 min per segment (Fig. 1). The segments were concatenated with no silence between them, continuing uninterrupted for a total of 3 min per block. The duration of each experimental session was approximately 2.5 h, which included electrode placement and rest breaks (one 15-min break occurring halfway through the recording session and shorter 5-min breaks as needed). Participants sat in a comfortable chair in an acoustically dampened room and were instructed to ignore the sounds and read a book during the testing session.

2.1.3. Stimuli

Ten pure tones (70 dB SPL, 50 ms duration, 5 ms rise/fall times) that differed only in pitch were used. Tones were presented bilaterally via insert earphones at a constant 150 ms stimulus onset asynchrony (SOA; onset to onset). There were five standard-deviant tone pairs, presented in separate blocks that were equiprobably distributed within the experiment. The deviant tones (466, 621, 830, 1109 and 1480 Hz, respectively) were 12% higher in frequency than their corresponding 'standard' tones (415, 554, 740, 988 and 1319 Hz). Stimuli were presented in an auditory oddball-type paradigm, with the standard tone presented 85% and the deviants 15% of the time. Deviants were presented in two ways; either a single tone had a higher pitch ('single deviant') or two successive tones had a higher pitch ('double deviant') than the standard. The segments within each block differed in the way the deviants were presented (Fig. 1). The first segment (Blocked Segment 1) had double deviants *only*, which occurred 7.5% of the time amongst the standards (30 double deviants, 15% deviants overall). In the second segment (Mixed Segment 2) single and double deviants were mixed within the segment, 5% double deviants and 10% single deviants (15% deviants overall). In the mixed segment, the occurrence of the deviants was pseudo-randomized. This was done so that we could examine the time course of the changes occurring in the processing of the double deviant when the single deviants were added. The first deviant in the mixed segment was a single deviant. The next occurrence of a deviant was a double deviant, and so on for three alternations of single and double deviants (a random number of standards occurred between consecutive deviant events, that is between single and double deviants). From then on, single and double deviants occurred in a random order (mixed within the standard tones) to the end of the segment (10 double deviants and 40 single deviants all together). The third segment (Blocked Segment 3) was

Stimulus Paradigm

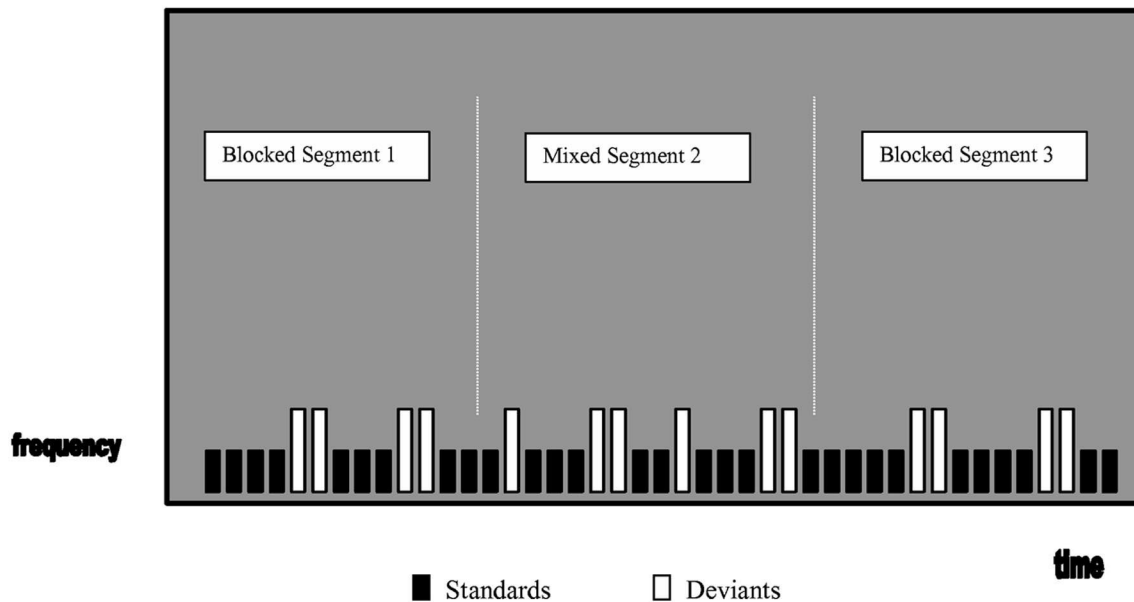


Fig. 1. Stimulus paradigm. Schematic diagram showing the characteristics of the blocked and mixed segments within the sound sequence. The height of the bars represents the frequency of the standard (black) and deviant (white) tones (y axis) across time (abscissa).

another segment in which only double deviants were presented amongst the standards (30 double deviants in all). The occurrence of deviants within the segments was randomized, separately for each segment, in each of the 25 stimulus blocks.

2.2. Recording and data analysis

Electroencephalographic (EEG) recordings were obtained from electrodes attached to the scalp at the following locations: Fz, Cz, Pz, F3, F4, FC1, FC2, C3, C4, P3, P4 (10–20 system) and the left and right mastoids (LM and RM, respectively). An electrode placed on the tip of the nose was used as the common reference. Horizontal eye movements were monitored, by recording the electrooculogram (EOG), using a bipolar electrode configuration between F7 and F8. Vertical EOG and eye movements were monitored between FP1 and an electrode placed below the left eye. The EEG was digitized at a rate of 250 Hz (0.05–100 Hz bandpass) and then filtered off-line (1.5–20 Hz). Epochs were 550 ms in duration, starting 100 ms before the onset of the tones. Epochs within which the response amplitude exceeded $\pm 100 \mu\text{V}$ at any recording site were rejected from subsequent processing, to remove trials contaminated by artifacts of non-cortical origin.

In order to analyze the time course of the ERP changes resulting from changing the context in the tone sequence, separately for each subject and segment, the double

deviants were grouped according to their position within the segment. For the blocked segments, the first six double deviants were averaged together across stimulus blocks (this average will be denoted as the response at the 'Beginning' of the segment), the next six double deviants were again averaged together (this average will be called the 'Within' segment response) and, finally the last six double deviants were averaged together (this average will be denoted as the response at the 'End' of the segment). For the mixed segments, the first half of the double deviants were analyzed in one group (Beginning) and the second half were analyzed in another (End). Single deviants in the mixed segment were grouped just as the double deviants in the blocked segments (i.e. Beginning, Within and End; six responses in each group).

The responses elicited by the standard tones preceding a deviant by two positions in the sequence were grouped and averaged in one-to-one correspondence with the deviant tones to determine whether there was a possible confound of temporal non-deviance-related changes associated with changing the context within each segment. No significant difference in the mean amplitudes was found for these standards at any position within or across the segments. Therefore, a mean of the standards across all segments and stimulus blocks was calculated and used for the standard comparison. MMNs were delineated by subtracting from each averaged deviant response, the mean standard-stimulus response.

The size of the MMN responses was estimated using the mean frontal (Fz) amplitude in the 116–156 ms interval of the deviant-minus-standard difference curves for the MMN elicited by the first of the successive deviant stimuli (Range 1) and in the 308–348 ms interval for the second of the successive deviant stimuli (Range 2). Amplitude measurements were referred to the mean amplitude in the 100-ms prestimulus period. One-sample, one-sided *t*-tests were used to verify the presence of the MMN component, separately for each peak, segment and position within the segment. One-way repeated-measure analyses of variance (ANOVA) were used to compare the deviant-minus-standard difference amplitudes in the MMN latency ranges within and across the different segments. For most statistical analyses, the ERP responses were re-referenced to the average of the two mastoids to estimate the full MMN response, except where explicitly noted that separate statistical tests have been conducted for the frontal (Fz) and the left mastoid (LM; using the original reference)

responses. Huynh–Feldt corrections were reported when appropriate.

3. Results

Fig. 2 displays the grand-averaged frontal (Fz) ERP responses elicited by the double deviant tones separately for each of the three segments and the position within the segments. Each deviant response is overlain with the mean standard response. Fig. 3 displays the grand-averaged frontal difference waveforms (the ERP response to the deviant minus that to the standard) in a similar structure. The double deviants in Segment 1 elicited one significant MMN component at the Beginning, Within and End of the segment (see Table 1 for the mean MMN amplitudes and statistical test results). The MMN can be seen as the negative waveform peaking at about 135 ms from stimulus

ERP Responses to Double Deviants

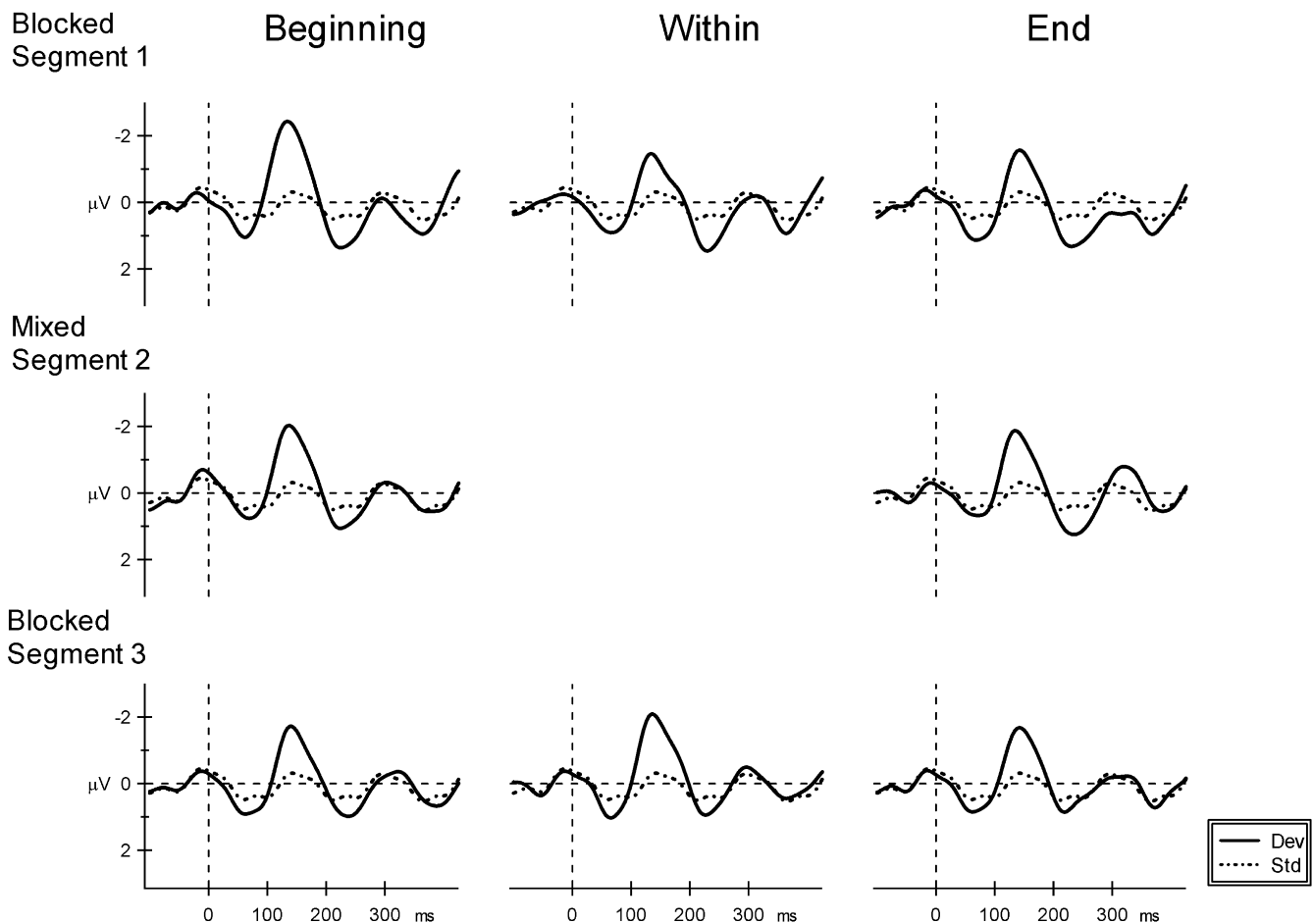


Fig. 2. Grand averaged frontal (Fz) ERPs elicited by the standards (dashed line) and double deviants (solid line) at the Beginning, Within and End positions of Segments 1, 2 and 3, separately.

Difference Waveforms for Double Deviants

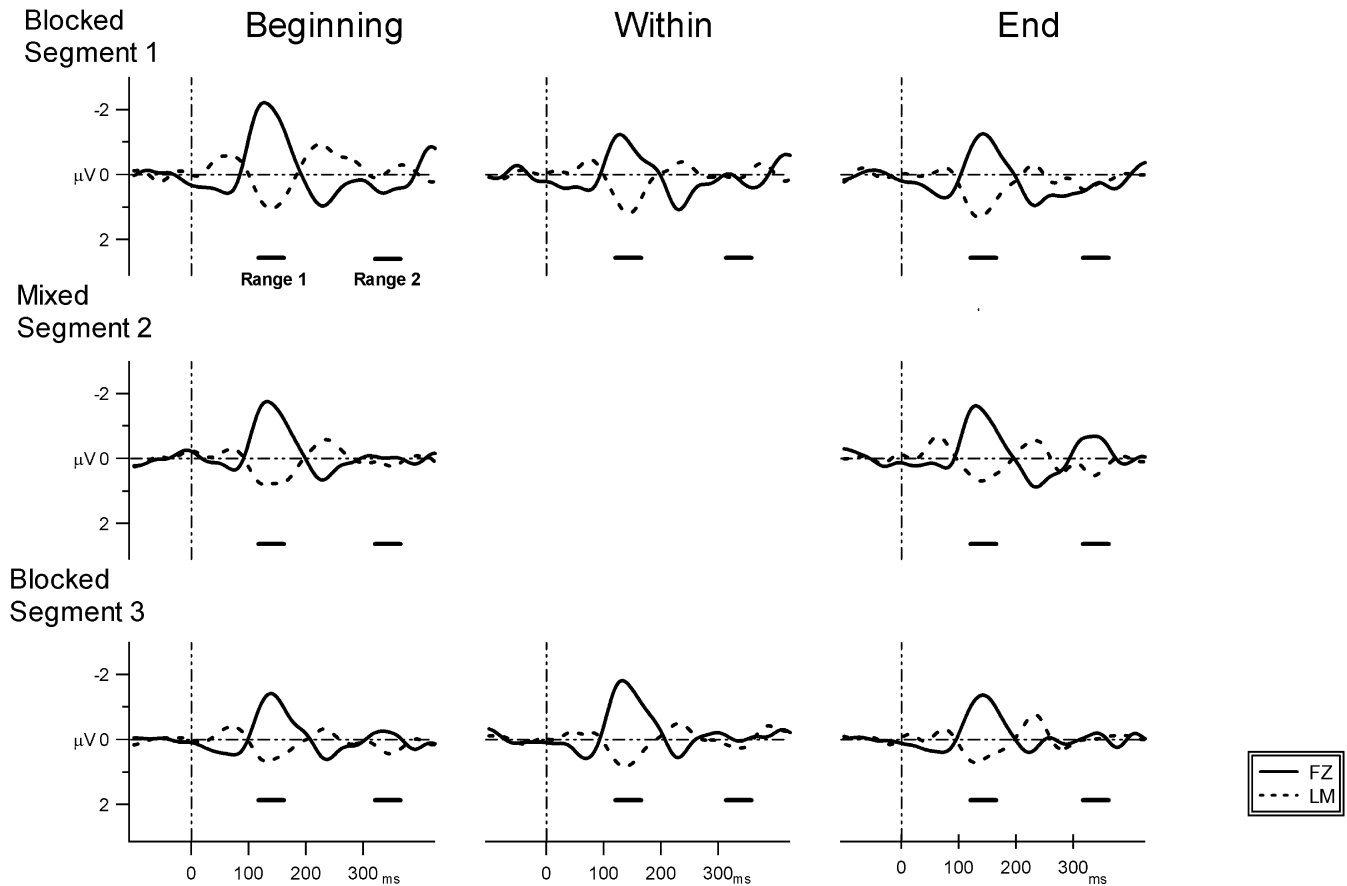


Fig. 3. Difference waveforms obtained by subtracting the ERPs elicited by the standard tones from the ERPs elicited by the double deviant tones at the Beginning, Within and End positions of the segments. The frontal (Fz, solid line) and mastoid (LM, dashed line) responses are overlain to show the scalp topography of the MMNs. Short horizontal bars mark the latency ranges for the two possible MMNs.

onset for all three positions of the segment appearing with inverted polarity at the left mastoid (LM).

In Segment 2, MMN was elicited by the first deviant of the double deviants both at the beginning and the end of the segment. The MMN peak latency was about 135 ms for both positions within the segment. The second deviant of the double deviants elicited a significant MMN only at the End of the segment, which peaked at about 320 ms from the onset of the first deviant stimulus (see Table 1, Fig. 3).

Two significant MMNs were elicited at the Beginning of Segment 3, but at the Within and the End positions of the segment, double deviants elicited only one MMN (Table 1). The MMNs elicited by the first deviant of the double deviants peaked at about 135 ms for the Beginning, 127 ms for the Within and 140 ms for the End positions of the segment. The MMN elicited by the second deviant of the double deviants, seen only at the Beginning of the segment, peaked at about 320 ms.

A one-way ANOVA comparing the deviant-minus-standard difference amplitude in Range 2 across the Ends of

the three segments showed that the Segment-2 amplitude (where MMN was present) was significantly larger than the amplitude in the other two segments ($F(2,16)=5.37$, $P<0.05$, ϵ , 0.68). This result shows that the presence of the single deviants had a significant effect on the elicitation of the second MMN.

A significant decrease in amplitude from the Beginning to the End position of the segments can be observed at the frontal electrode site (Fz) for the MMN elicited by the first deviant of the double deviants [$F(1,8)=11.4$, $P<0.01$], but no significant amplitude change was observed at the left mastoid site [$F(1,8)<1$, $P>0.65$]; Fig. 3), as was revealed by a two-way repeated-measures ANOVA with factors of Position (Beginning vs. End for Segments 1 and 2, Within vs. End for Segment 3) \times Segment (1 vs. 2 vs. 3). The Within position was used instead of Beginning for Segment 3 in the above ANOVA because we took the Within position as the true beginning of Segment 3 (see explanation below).

The effect resulting from adding single deviants, the

Table 1
Mean deviant minus standard difference amplitudes in the MMN latency range

Deviant type	Segment 1			Segment 2		Segment 3		
	Beginning	Within	End	Beginning	End	Beginning	Within	End
Double								
Fz	-2.12	-1.05	-1.06	-1.72	-1.42	-1.30	-1.67	-1.29
Range 1	(1.54)	(0.93)	(0.99)	(0.64)	(0.72)	(0.89)	(1.07)	(0.75)
112–156 ms	**	**	**	**	**	**	**	**
LM	0.88	1.04	1.23	0.73	0.77	0.61	0.80	0.68
Range 1	(0.46)	(0.93)	(0.90)	(0.62)	(0.58)	(0.46)	(0.40)	(0.99)
112–156 ms								
Fz	0.38	0.14	0.45	-0.20	-0.58	-0.27	-0.01	-0.21
Range 2	(0.62)	(0.37)	(0.59)	(0.72)	(1.03)	(0.66)	(0.79)	(0.36)
304–336 ms					**	*		
LM	-0.08	0.12	0.44	0.09	0.35	0.29	0.31	0.08
Range 2	(0.33)	(0.50)	(0.45)	(0.54)	(0.38)	(0.40)	(0.27)	(0.78)
304–336 ms								
Single	Segment 2							
	Beginning	Within	End					
Fz	-1.48	-1.52	-1.30					
112–156 ms	(1.06)	(0.93)	(1.23)					
	**	**	**					
LM	0.99	0.89	0.77					
112–156 ms	(0.46)	(0.30)	(0.76)					

All values expressed as means with standard deviations in parenthesis. *, $P < 0.05$; **, $P < 0.01$.

change from one to two MMNs was seen at the End position of Segment 2, while the effects resulting from the cessation of the single deviants, the change from two to one MMN was seen at the Within position of Segment 3. In Segment 3, the Within-position ERP response, not the Beginning-position one, matches the response obtained in the Beginning position of the other segments. The Beginning position of Segment 3 still shows two MMNs (as it was at the End position of Segment 2), whereas the Within position shows only one MMN (as also is evident at the End position of Segment 3). Moreover, the frontal (Fz) amplitude of the first MMN increased from the Beginning position of Segment 3 to the Within position, thus reaching the level found for the Beginning position of the other two segments ($F(2,16)=1.3$, $P > 0.25$, ϵ , 1.00; one-way repeated-measures ANOVA of the frontal (Fz) first-MMN amplitudes comparing the Beginning positions of segments 1 and 2 and the Within position of Segment 3).

Fig. 4 displays the grand mean responses and corresponding difference waveforms obtained for the single deviants in the second segment of the stimulus blocks. The statistically significant negative waveforms that can be observed peaking at around 135 ms from stimulus onset in the Beginning, Within and End positions of the segment are MMN responses (Table 1). The change in MMN amplitude elicited by the single deviants in Segment 2 as a function of the position of the single deviants within the segment did not reach significance either at Fz or LM

[$F(2,16)=0.78$ and 0.70 , respectively] although the frontal MMN amplitude was smaller by the end of the block (Fig. 4). Furthermore, note on the single deviant difference waveforms (bottom of Fig. 4) that the ERP signal in Range 2 (that is, in the latency range in which the second MMN may appear in the double-deviant responses) is close to the baseline. Finally, deviants in Segment 2 (either single or double deviants) elicited no additional ERP components (e.g. attention-related components) compared with the ERP responses observed for deviants in the other two segments (compare Figs. 2 and 4). These two observations support the notion that in Segment 2, the second deviant of the double-deviant stimuli elicited a genuine MMN component. The change in the context affected the MMN response to the second deviant of the double-deviant stimulus and not some late, possibly attentional component elicited by the first deviant of the double deviant stimuli.

4. Discussion

A dynamic process of sensory updating was demonstrated by changes in the brain's response to the same stimulus event (the double deviants). The significant changes in brain response corresponded with contextual changes in the sound sequence within which the double deviants were encountered. By changing the context surrounding the double deviants we changed the way they

Single Deviant MMNs - Segment 2

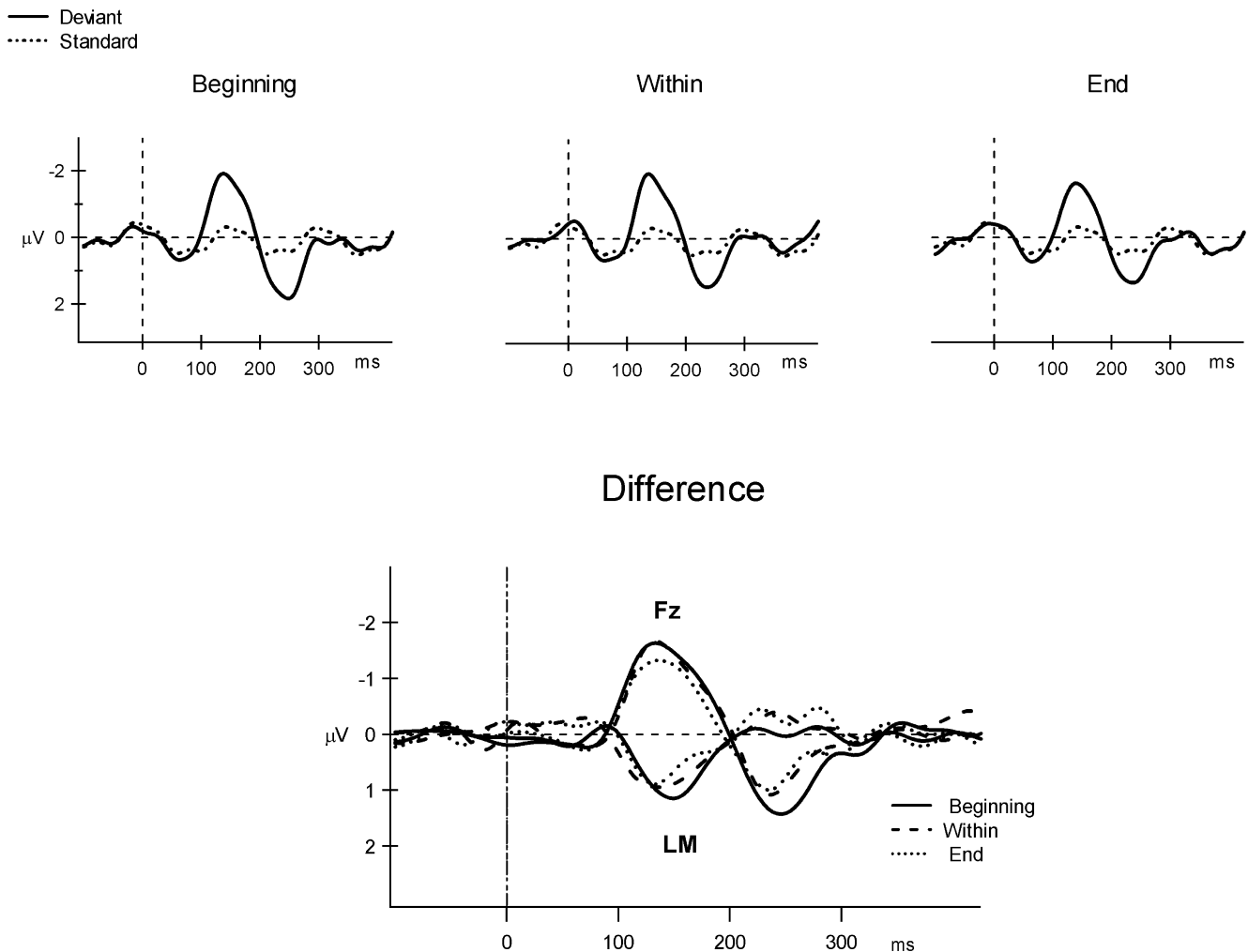


Fig. 4. Grand averaged ERPs elicited by the single deviants in the Middle Segment 2. The upper panel displays the responses to the standard (dotted lines) and deviant (solid line) tones for the Beginning, Within and End positions of the segment. The bottom panel displays the difference waveforms at the frontal (Fz) and mastoid (LM) sites, overlaying the responses elicited at the Beginning (solid line), Within (dashed line) and End (dotted line) positions of the segment.

were processed. Depending on the presence of single deviants, the double deviants elicited one or two MMNs.

The double deviants, occurring successively within a 150-ms time period elicited one MMN from their first occurrence in the stimulus block. This indicates that the double deviants were integrated into a single event at the beginning of the sound sequence. An analogous finding was obtained by Bregman [2], who demonstrated that the perception of a sound sequence starts out as an integrated stream and that segregating the sequence into two or more streams requires several seconds for evidence of the presence of distinct sound sets to accumulate. This suggests that the auditory system initially attributes all sounds to the same source (integration) and only after sufficient information is obtained can two or more streams emerge in perception (segregation). The present results are consistent

with Bregman's hypothesis suggesting that integration of the incoming auditory information is the 'default' organization of closely spaced auditory events.

As expected on the basis of our previous results [Sussman and Winkler, unpublished data], double deviants elicited one MMN when they occurred in the blocked segments and two MMNs when they occurred in the mixed segment. What was remarkable was how closely the effects of contextual change followed the onset or cessation of the single deviants in the sequence. In less than a minute, within the minute long Segment 2 (when the single deviants appeared in the sound sequence), two successive MMNs emerged in the double deviant responses and within the next minute segment (Blocked Segment 3) the response to the double deviants went back to one MMN. This fast accommodation to changes in the sensory input

suggests that there is a dynamic process of sensory updating continuously 'on alert' in the auditory system.

The effects of context change occurred within a short time, but not immediately, whether new information was added (the onset of single deviants at the beginning of Segment 2) or whether current information ceased (the cessation of the single deviants at the beginning of Segment 3). The elicitation of the second MMN in the beginning of the Blocked Segment 3 and the subsequent loss of this MMN within the segment established that it takes time for the auditory system to determine that a source has truly ceased, rather than temporarily paused². This would suggest that there is a biasing of the system to maintain the organization that is current until enough information is gained to establish that the context changed. In natural (complex) auditory environments, this bias could regulate the system so that organization of auditory input is not disturbed by chance occurrences. These conclusions are consistent with previous studies showing that the auditory system adapts quite quickly to changes in the acoustic environment, using sufficient amount of information to determine when the changes reflect true contextual changes [3,7,16,20].

The amplitude of the MMN (to the first physical deviation) at the change points (i.e. at the beginning of each segment — though somewhat later in Segment 3, see the discussion above) was significantly larger than the amplitude of the MMN observed at the end of the segments. This decrease in amplitude was seen at the frontal electrode sites but not at the mastoid sites. This latter finding corroborates evidence from previous studies that concluded that there is more than one generator contributing to the observed MMN component [5], suggesting that determinants of frontal and supratemporal MMN-generating processes may differ [1,6,8,14]. One interpretation is that the supratemporal source (best shown by electrode sites located at the mastoids) may reflect the immediate consequence of stimulus change generated in auditory cortex, whereas the frontal MMN (partly indexed by electrode sites located in the fronto-central region of the scalp) may reflect a call for attention switching. In the current study, the similar MMN amplitudes at the mastoid site across each segment could be explained by the fact that the physical deviancy between the standard and the deviant is constant throughout the experiment. In contrast, the reduction of the frontal MMN amplitude from the beginning to the end of each segment could mean that by repetition the deviant stimulus gradually lost some of its importance. However, the importance of the deviance had to be reevaluated when the context changed (i.e. at the beginning of each segment). The increased frontal re-

sponse raises the chance that a switch of attention to the new information will occur.

Change is an important cue for the auditory system. Even while we attend to one part of the sensory input (such as reading a book) we still have information about changes that occur in the surrounding environment. The present results suggest that the auditory system monitors sound for changes in the input, even if it is not in our immediate focus of attention. Changes occurring in the background may signal the start of new information, which may require further analysis or indicate that some action is necessary. The present experiment modeled a natural situation, in which one voluntarily focuses on a given source of information, while subtle changes occur in a different sensory stream. Subjects had no task related to the sounds; they were reading a book while the sounds were presented to them. The stimulus driven change in context in and of itself (i.e. the addition of the single deviants in Segment 2) did not capture attention, as was indicated by the lack of additional or increased-amplitude ERP components in Segment 2 (compared with the other two segments), such as the P3a component (which is associated with attention switching). The absence of P3a in Segments 2 and 3 suggests that the subjects did not become aware of the contextual changes occurring in the auditory stream. Thus, the present results support the hypothesis that the auditory system maintains a representation of the context for sound streams whether or not they are relevant to the ongoing behavior [20]. The MMN response is probably part of the system that monitors the auditory environment in its effort to track changes that may affect the formation of auditory events or objects [18]. The present data provide evidence of a dynamic sensory updating of the acoustic information on-line, as the changes are happening.

Acknowledgements

This research was supported by the National Institutes of Health (Grant R01 DC04263) and the Hungarian National Research Fund (OTKA T034112). We thank Dr. Mitchell Steinschneider for his comments and suggestions.

References

- [1] K. Alho, Cerebral generators of mismatch negativity (MMN) and its magnetic counterpart (MMNm) elicited by sound changes, *Ear Hear* 16 (1995) 38–51.
- [2] A.S. Bregman, Auditory streaming is cumulative, *J. Exp. Psychol. Human Percept. Perf.* 4 (1978) 380–387.
- [3] N. Cowan, I. Winkler, W. Teder, R. Näätänen, Memory prerequisites of the mismatch negativity in the auditory event-related potential (ERP), *J. Exp. Psychol. Learn. Mem. Cogn.* 19 (1993) 909–921.
- [4] I. Czigler, I. Winkler, Preattentive auditory change detection relies on unitary sensory memory representations, *NeuroReport* 7 (15) (1996) 2413–2417.

²The temporal resolution of the present paradigm was lower when establishing the onset of the effect of the addition of the single deviants due to the lower number of double deviants in the Mixed Segment 2 than in the Blocked Segments 1 and 3.

- [5] M.H. Giard, F. Perrin, J. Pernier, P. Bouchet, Brain generators implicated in processing of auditory stimulus deviance: A topographic event-related potential study, *Psychophysiology* 27 (1990) 627–640.
- [6] I.P. Jääskeläinen, E. Pekkonen, J. Hirvonen, P. Sillanauke, R. Näätänen, Mismatch negativity subcomponents and ethyl alcohol, *Biol. Psychol.* 43 (1996) 13–25.
- [7] J. Horváth, I. Czigler, E. Sussman, I. Winkler, Simultaneously active preattentive representations of local and global rules for sound sequences in the human brain. *Cogn. Brain Res.* (in press).
- [8] M. Molnár, J.E. Skinner, V. Csépe, I. Winkler, G. Karmos, Correlation dimension changes accompanying the occurrence of the mismatch negativity and the P3 event-related potential component, *Electroenceph. Clin. Neurophysiol.* 95 (1995) 118–126.
- [9] R. Näätänen, *Attention and Brain Function*, Erlbaum, Hillsdale, NJ, 1992.
- [10] R. Näätänen, A.W.K. Gaillard, S. Mäntysalo, Early selective attention effect on evoked potential reinterpreted, *Acta Psychol.* 42 (1978) 313–329.
- [11] R. Näätänen, M. Tervaniemi, E. Sussman, P. Paavilainen, I. Winkler, Cognitive process at the sensory level in audition, *Trends Neurosci.* 24 (2001) 283–288.
- [12] R. Näätänen, I. Winkler, The concept of auditory stimulus representation in cognitive neuroscience, *Psychol. Bull.* 125 (1999) 826–859.
- [13] T.W. Picton, C. Alain, L. Otten, W. Ritter, W. Achim, A. Achim, Mismatch negativity: different water in the same river, *Audiol. Neuro-Otol.* 5 (2000) 111–139.
- [14] T. Rinne, K. Alho, R. Ilmoniemi, J. Virtanen, R. Näätänen, Separate time behaviors of the temporal and frontal mismatch negativity sources, *NeuroImage* 12 (2000) 14–19.
- [15] W. Ritter, D. Deacon, H. Gomes, D.C. Javitt, H.G. Vaughan Jr., The mismatch negativity of event-related potentials as a probe of transient auditory memory: a review, *Ear Hear* 16 (1995) 52–67.
- [16] E. Schröger, On the detection of auditory deviations: a preattentive activation model, *Psychophysiology* 34 (1997) 245–257.
- [17] E. Sussman, I. Winkler, W. Ritter, K. Alho, R. Näätänen, Temporal integration of auditory stimulus deviance as reflected by the mismatch negativity, *Neurosci. Lett.* 264 (1–3) (1999) 161–164.
- [18] I. Winkler, I. Czigler, Mismatch negativity: deviance detection or the maintenance of the ‘standard’, *NeuroReport* 9 (1998) 3809–3813.
- [19] I. Winkler, I. Czigler, M. Jaramillo, P. Paavilainen, R. Näätänen, Temporal constraints of auditory event synthesis: evidence from ERPs, *NeuroReport* 9 (3) (1998) 495–499.
- [20] I. Winkler, G. Karmos, R. Näätänen, Adaptive modeling of the unattended acoustic environment reflected in the mismatch negativity event-related potential, *Brain Res.* 742 (1996) 239–252.