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MMN or no MMN: No magnitude of deviance effect on the MMN amplitude

JÁNOS HORVÁTH,[a,b] ISTVÁN CZIGLER,[b] THOMAS JACOBSEN,[a] BURKHARD MAESS,[c] ERICH SCHRÖGER,[a] AND ISTVÁN WINKLER[b]

[a]Institute of Psychology I, University of Leipzig, Leipzig, Germany
[b]Institute for Psychology, Hungarian Academy of Sciences, Budapest, Hungary
[c]Max-Planck-Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

Abstract

Based on results showing that the ''deviant-minus-standard'' estimate of the mismatch negativity (MMN) amplitude increases with increasing amounts of deviance, it has been suggested that the MMN amplitude reflects the amount of difference between the neural representations of the standard and the deviant sound. However, the deviant-minus-standard waveform also includes an N1 difference. We tested the effects of the magnitude of deviance on MMN while minimizing this N1 confound. We found no significant magnitude of deviance effect on the genuine MMN amplitude. Thus we suggest that the average MMN amplitude does not reflect the difference between neural stimulus representations; rather it may index the percentage of detected deviants, each of which elicits an MMN response of uniform amplitude. These results are compatible with an explanation suggesting that MMN is involved in maintaining a neural representation of the auditory environment.

Descriptors: ERP, Mismatch negativity (MMN), N1, Magnitude of deviance, Frequency change, Auditory change detection, Stimulus representation, Memory updating, Attention switching

The mismatch negativity (MMN) auditory event-related potential (ERP) is elicited when a sound violates a previously detected auditory regularity (Näätänen, Gaillard, & Mäntysalo, 1978; for recent reviews, see Kujala, Tervaniemi, & Schröger, 2007; Näätänen, Jacobsen, & Winkler, 2005; Näätänen & Winkler, 1999). Sounds complying with the regularity are termed *standards*; those violating it are termed *deviants*. MMN has been suggested to reflect deviation of the incoming stimulus from the memory representation of the standard sound (Näätänen, 1990) or from the sound input predicted by a neural model encoding the detected regularities (Winkler, in press; Winkler, Karmos, & Näätänen, 1996). MMN is most commonly studied in the auditory oddball paradigm, in which a repeating sound is occasionally exchanged for a different sound. Results of some previous studies suggested that the MMN amplitude increases whereas the peak latency decreases with increasing separation between the standard and the deviant sounds (Berti, Roeber, & Schröger, 2004; Näätänen, Simpson, & Loveless, 1982; Pakarinen, Takegata, Rinne, Huotilainen, & Näätänen, 2007; Sams, Paavilainen, Alho, & Näätänen, 1985; Tiitinen, May, Reinikainen, & Näätänen, 1994). The peak latency effect appears to be more reliable than the amplitude effect (Näätänen & Gaillard, 1983; Schröger & Winkler, 1995). MMN amplitude and peak latency have often been assessed from difference waves obtained by subtracting the standard–stimulus ERP from the deviant–stimulus response. However, the deviant-minus-standard difference is known to sum contributions from MMN and N1 (Jacobsen & Schröger, 2001; Schröger & Wolff, 1996; for a review, see Kujala et al., 2007). Therefore, the effects of the magnitude of deviance attributed to MMN may fully or partly reflect effects on the N1 amplitude. The goal of the present study was to retest the effects of the magnitude of deviance on the MMN amplitude and peak latency while minimizing the N1 confound.

The auditory N1 wave is elicited by abrupt changes in spectral sound energy (for a review, see Näätänen & Picton, 1987). N1 sums activation from several brain areas, including the auditory cortex (the ''supratemporal'' N1 component; see Vaughan & Ritter, 1970; for the generator structure within auditory cortex, see Lü, Williamson, & Kaufman, 1992b; Sams, Hari, Rif, & Knuutila, 1993). Although a large part of the N1 response is not stimulus specific (Hari et al., 1987, Näätänen, 1990), the location and parameters of some N1 subcomponents are sensitive to primary acoustic features, such as frequency, intensity, interaural time difference, and so forth (Bertrand, Perrin, Echallier, & Pernier, 1988; Jacobson, Lombardi, Gibbons,

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Address reprint requests to: János Horváth, Institute of Psychology I, University of Leipzig, Seeburgstr. 14-20, D-04103 Leipzig, Germany. E-mail: horvath@cogpsyphy.hu

Ahmad, & Newman, 1992; McEvoy, Hari, Imada, & Sams, 1993; Pantev, Hoke, Lehnertz, & Lütkenhöner, 1989; Pantev et al., 1988; Roberts & Poeppel, 1996; Romani, Williamson, & Kaufman, 1982). Therefore, subtracting ERP responses elicited by two different sounds can result in an N1 difference. Furthermore, the N1 shows a strong response decrement to sounds presented in short succession (Callaway, 1973; Näätänen & Picton, 1987; Ritter, Vaughan, & Costa, 1968), which may be due to adaptation (May et al., 1999; Ulanovsky, Las, Farkas, & Nelken, 2004), habituation (Lü et al., 1992b; Maclean, Ohman, & Lader, 1975), or refractoriness (Budd, Barry, Gordon, Rennie, & Michie, 1998; Ritter et al., 1968). Again, although part of the response decrement is not stimulus specific (Näätänen, 1990; Näätänen & Picton, 1987), stimulus–specific response decrements have also been observed (Cowan, Winkler, Teder, & Näätänen, 1993; Hari et al., 1987; Lü, Williamson, & Kaufman, 1992a). Because in the oddball paradigm, standard stimuli are typically presented 5 to 20 times more often than deviants, the stimulus–specific response decrement is usually significantly larger for standard than for deviant stimuli. This can result in an N1 difference between standard and deviant ERPs, thus affecting deviant-minus-standard difference waveforms. Therefore, the deviant-minus-standard difference sums two different effects, one resulting from memory-based deviance detection (MMN), the other from differential N1 response decrements (Jacobsen & Schröger, 2001, 2003; Jacobsen, Schröger, & Horenkamp, 2003; Jacobsen, Schröger, Horenkamp, & Winkler, 2003; Maess, Jacobsen, Schröger, & Friederici (2007); Näätänen & Alho, 1997; Schröger, 1997b; Schröger & Wolff, 1996; for reviews, see Kujala et al., 2007; Näätänen et al., 2005; for a related distinction of comparator and noncomparator accounts of the orienting response see also Siddle, 1991; for similar visual ERP effects, see also Czigler, Balázs, & Winkler, 2002; Pazo-Alvarez, Amenedo, & Cadaveira, 2004).

Tiitinen et al. (1994) quantified the dependence of the deviant-minus-standard difference amplitude and peak latency on the magnitude of frequency deviance. These authors found that the deviant-minus-standard difference amplitude was proportional to the logarithm of frequency deviance and that the reaction time in an active version of the same oddball paradigm followed the peak of the difference waveform by a constant delay at all levels of deviation (i.e., the two functions were parallel; for corroborating evidence regarding the correlation between the MMN peak latency and reaction time in a deviance detection task, see Novak, Ritter, & Vaughan, 1992a, 1992b; Novak, Ritter, Vaughan, & Wiznitzer, 1990; for reviews, see Näätänen & Winkler, 1999; Schröger, 1997a). These results were taken to mean that MMN amplitude reflects the amount of perceived difference between the neural representations of the standard and the deviant sound (Tiitinen et al., 1994; for a review, see Näätänen & Alho, 1997). This suggestion is also compatible with the hypothesized role of MMN in calling for the further processing of deviant auditory events (Näätänen, 1990, 1992), because sounds widely deviating from the preceding sequence are more likely to capture attention and to elicit the ERP correlates of attention switching (P3a; for reviews, see Escera, Alho, Schröger, & Winkler, 2000; Friedman, Cycowicz, & Gaeta, 2001; Polich & Criado, 2006). If MMN was involved in initiating an attention switch, then a larger MMN signal is probably more effective than a smaller one in achieving the redirection of attention (Näätänen, 1990, 1992; Schröger, 1997a; for a review of the supporting evidence, see Escera et al., 2000). However, Rinne, Särkkä, Degerman, Schröger, & Alho (2006) have found dissociation between MMN and P3a (for compatible evidence, see Winkler, Tervaniemi, Schröger, Wolff, & Näätänen, 1998) and instead, showed that P3a elicitation was probably related to the amplitude of N1 response (for a similar view, see Campbell, Winkler, & Kujala, 2007; but see Muller-Gass, Macdonald, Schröger, Sculthorpe, & Campbell, in press).

Increasing the acoustic separation between the standard and the deviant sound decreases the overlap between the afferent neuronal populations activated by these two sounds. As a consequence, more neurons will respond vigorously to the deviant sound (i.e., the response decrement specific to the deviant sound will be smaller) and the deviant-minus-standard ERP difference will increase. Thus the observed correlation between the magnitude of deviance and P3a elicitation may be mediated by N1, an effect that was also included in previous models of change detection (Näätänen, 1990; Schröger, 1997a). This explanation can also account for the effects of the magnitude of acoustic deviance on behavioral and autonomic measures of distraction (Escera et al., 2000; Lyytinen, Blomberg, Näätänen, 1992).

It is thus possible that the effect of the magnitude of deviance on the amplitude of the deviant-minus-standard difference waveform represents an effect on the genuine MMN component or on the N1-decrement or on both. For maximal compatibility with previous results, we employed stimulus parameters from the seminal study of Tiitinen et al. (1994), but added a control condition to eliminate N1-effect confounds in estimating the MMN parameters. The control condition was the one originally proposed by Schröger and Wolff (1996), which provides a robust estimate of the genuine MMN response by substantially reducing the bias resulting from N1 effects. In this control condition, standard stimuli of the oddball sequence are replaced by random sounds. These replacement sounds differ from each other in the same stimulus feature (frequency in the present study) as the standard and the deviant in the corresponding oddball sequence with the acoustic separation between the replacement and the control sound (the deviant of the oddball sequence) equal to or larger than that between the standard and the deviant sound (Jacobsen & Schröger, 2001; see Figure 1). Deviant–stimulus responses recorded in the oddball sequence are then compared with those elicited by physically identical control sounds (see Figure 1), thus eliminating the ERP difference stemming from acoustic differences (see above). Because there is no frequent sound (standard) in the control sequence, the control sound does

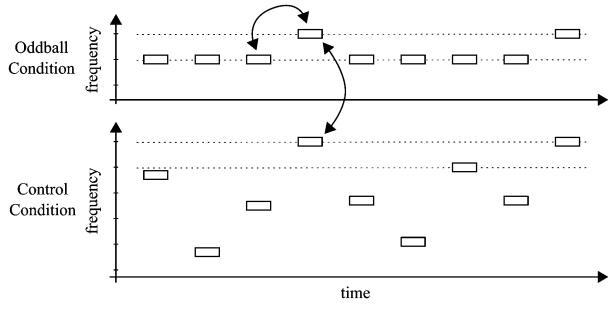

Figure 1. Schematic diagram of the auditory oddball paradigm with frequency deviants and the corresponding control stimulus sequence. The deviant versus standard and deviant versus control comparisons are shown by arrows. Horizontal gray dashed lines denoting deviant and standard frequencies are shown for comparison.

not violate any regularity and thus elicits no MMN. As for the reduction of the N1 confound, deviant and control sounds are delivered with the same sequential and temporal probability, which promotes the elicitation of equal N1 amplitudes. However, due to the, on average, larger acoustic separation between the control and the replacement sounds compared to the separation between the deviant and the standard, stimulus–specific refractoriness may be higher for the deviant than for the corresponding control sound and, therefore, control sounds may elicit a higher amplitude N1 than deviants (Butler, 1968; Näätänen et al., 1988; for a review, see Näätänen & Picton, 1987). Therefore, the deviant-minus-control derivation may slightly underestimate the MMN amplitude.

Methods

Participants

Twelve healthy volunteers (6 female, 18–24 years of age, mean 20.6 years) participated in the experiment. The participants gave written informed consent after the nature of the experiment was explained to them. They received monetary compensation for participating in the study. Before the experiment, the participants' hearing was assessed with an audiometer (Mediroll SA-5). No participant had a pure-tone frequency threshold higher than 20 dB SPL in the frequency range used in the experiment (250–2000 Hz), and no significant asymmetry (i.e., a threshold difference of 15 dB or more) was found between the hearing thresholds for two ears in any of the participants.

Stimuli and Procedure

Sequences of sinusoid tones were presented through headphones (Sennheiser, SD-25). The duration of the tones was 60 ms including 10 ms rise and 10 ms fall times. The onset-to-onset interval between stimuli was 200 ms. Tone intensity was adjusted to 65 dB sensation level (above threshold hearing level), separately for each participant.

There were four oddball and four corresponding control conditions. In oddball conditions, 95% of the tones were standard tones (1000 Hz), 5% were deviants (1020, 1040, 1127, and 1320 Hz in Oddball 1, 2, 3, and 4, respectively). For each oddball condition, a corresponding control condition was used. In the control sequences, 5% of the tones were control tones having the same frequency as the deviant in the corresponding oddball condition. Standard tones were replaced by six tones of different frequencies (''replacement'' tones), each lower than the deviant, presented with 15.83% probability, each in a random order. Six different replacement tones were demonstrated to be sufficient to eliminate the N1 difference in a similar paradigm (i.e., increasing the number of replacement tones from six to nine did not result in a substantial change in the N1 amplitude; see Jacobsen, Schröger, Horenkamp, & Winkler, 2003). In each condition, a different set of replacement tones was used. Frequencies for these tones were selected so that the ratio between neighboring frequencies was equal to the deviant/standard frequency ratio in the corresponding oddball sequence. Each control sequence included the standard (1000 Hz) frequency as well (see Table 1). Given the frequency resolution function of the auditory system, by keeping the frequency ratio equal across the control conditions, the effect of the replacement tones on the control tone N1 can be assumed to show a similar function as the effect of standard tones on the deviant N1. Each condition consisted of three stimulus blocks with 1533 stimuli each. Overall, 230 deviant and 230 control tones were delivered in each condition.

Table 1. *Stimulus Parameters (Frequency and Sequential Probability) for each Condition*

	Oddball condition		Control condition	
Magnitude of deviance	Tone frequencies (Hz)	Probability (%)	Tone frequencies (Hz)	Probability (%)
20 Hz	1020.0	5.00%	1020.0	5.00%
	1000.0	95.00%	1000.0	15.83%
			980.4	15.83%
			961.2	15.83%
			942.3	15.83%
			923.8	15.83%
			905.7	15.83%
40 Hz	1040.0	5.00%	1040.0	5.00%
	1000.0	95.00%	1000.0	15.83%
			961.5	15.83%
			924.6	15.83%
			889.0	15.83%
			854.8	15.83%
			821.9	15.83%
127 Hz	1127.0	5.00%	1127.0	5.00%
	1000.0	95.00%	1000.0	15.83%
			887.3	15.83%
			787.3	15.83%
			698.6	15.83%
			619.9	15.83%
			550.0	15.83%
320 Hz	1320.0	5.00%	1320.0	5.00%
	1000.0	95.00%	1000.0	15.83%
			757.7	15.83%
			573.9	15.83%
			434.8	15.83%
			329.4	15.83%
			249.5	15.83%

The experiment was carried out in two sessions separated by less than 8 days. In each session two oddball and two corresponding control conditions were delivered to the participant. The order of the conditions was randomized across participants. Corresponding oddball and control blocks were presented in an interwoven sequence (either oddball, control, control, oddball, oddball, control or the opposite order, randomized separately for each condition and participant). Consecutive stimulus blocks were separated by short breaks.

During the EEG recording, participants watched a silent, subtitled movie of their choice and they were instructed to ignore the tones. An active behavioral experiment was administered 10–20 min after the end of the second session. During the break, the electrodes were dismounted. Participants were presented with one stimulus block of each of the oddball conditions in randomized order. They were instructed to attend the tones and to press a response button when detecting a deviant. The instruction emphasized both speed and accuracy.

Analysis of Performance Data

To avoid contamination from interference between closely spaced target tones, only responses to deviants separated by at least four standard tones were analyzed. Only responses in the 100–800-ms interval following the onset of a deviant were accepted as hits. For calculating false alarm rate and d', a subset of standard tones was selected: The selected standards were sepa-

rated from deviants as well as from each other by at least four other standard tones. Responses were then analyzed in the 100–800-ms-long poststimulus interval for the selected standards. This procedure adjusted for the acceptable response rate (maximally once in a 700-ms interval; see above), which was longer than the stimulus presentation rate (one stimulus per 200 ms). To avoid infinite values in d' calculations, the hit rate was adjusted to $1-(1/(2N))$ when it was actually 1 (i.e., all targets were detected) and, similarly, the false alarm rate was adjusted to $1/(2N)$ when it was actually 0 (no false alarms; for the validation of this procedure, see Macmillan & Creelman, 1991). Reaction times (RT) and d' values were analyzed in one-way analyses of variance (ANOVA) with the factor of condition (four levels). All significant results are discussed.

EEG Recording and Analysis

EEG was recorded with Ag/AgCl electrodes by Nuamps amplifier (Neuroscan, Inc.) with a sampling rate of 500 Hz and filtered online between 0 and 40 Hz. Electrodes were placed on the scalp at locations Fz, Cz, Pz, T3, T4, C3, C4, Fp1, Fp2, F7, F8, F3, F4, O1, O2, T5, T6, P3, P4, FC1, FC2, CP1, CP2, FT3, FT4, TP3, and TP4 (according to the 10% system; Nuwer et al., 1998), on the two mastoids (left: Lm and right: Rm), and on the halfway points of the lines connecting the mastoids and the inion (left: OM1 and right: OM2). The reference electrode was attached to the tip of the nose. Horizontal eye movements were monitored between electrodes placed lateral to the outer canthi of the two eyes; vertical eye movements were monitored between electrodes placed above and below the right eye.

EEG was bandpass filtered off-line (2–20 Hz). Epochs were 600 ms long, including a 200-ms-long prestimulus interval. The average signal amplitude measured during the 200-ms prestimulus interval was used as baseline. Epochs with a signal range exceeding 75 μV at any EEG or EOG channel were discarded from the analyses. To avoid carryover from preceding deviants, only ERP responses to those deviants, standards, and control tones were analyzed that were preceded by at least two standard (Conditions 1–4) or two replacement tones (Control Conditions 1–4). Two ways of analyses were carried out: (1) We replicated the method in Tiitinen et al. (1994) for direct comparison with their results. In this analysis, we determined the latency of local minima (negative peak) at Fz in the 75–250-ms interval, separately for each condition from the group–averaged deviant-minus-standard difference waveform. Amplitude measures were then calculated as the average voltage at Fz in a 20-ms-long interval centered on these peaks. (2) The same procedure was carried out on the deviant-minus-control difference waveforms, again, separately for each condition. We also measured the frontal (Fz) deviant-minus-standard and deviant-minus-control peak latencies separately for each subject at each different magnitude of deviance. In three subject/deviance cases altogether, no local minimum could be discerned in the individual average difference waveforms. In these cases we took the latency of the absolute minimum in the 75–250-ms interval. When two distinct negative difference peaks could be discerned, we chose the one falling closer to the peak observed on the corresponding group–averaged waveform. The two sets of amplitude and two sets of latency measurements were analyzed in two-way, repeated–measures ANOVAs with factors of derivation (deviant-minus-standard vs. deviant-minus-control) and deviance magnitude (20, 40, 127, 320 Hz). Greenhouse–Geisser correction was applied where appropriate; all significant results, degrees of freedom correction factors (ε), and partial eta-squared (η^2) effect size values are reported.

Table 2. *Reaction times, Hit and False Alarm Rates, and d′ Values Obtained at the Four Levels of Deviations (Standard Errors in Parentheses)*

Magnitude of deviance (Hz)	RT (ms)	Hit rate (%)	False alarm rate (%)	d′
20	451 (9)	79.7 (3.0)	1.7 (0.9)	3.25 (0.19)
40	385 (14)	90.6 (2.1)	0.8 (0.1)	3.98 (0.20)
127	322 (10)	97.4 (0.7)	0.4 (0.1)	4.75 (0.11)
320	300 (12)	96.1 (1.0)	0.4 (0.1)	4.62 (0.13)

Results

Performance Measures

Performance indices obtained in the active part of the experiment are summarized in Table 2 and Figure 4, below. One-way ANOVA of the d' values showed an effect of condition, $F(3,33) = 21.33$, $\eta^2 = .66$, $p < .001$ (Figure 4, below, third panel). Post hoc Tukey HSD tests showed that d' values differed between each pair of deviation magnitudes by at least $p < .05$, except between 127-Hz and 320-Hz deviations. One-way ANOVA of the RTs showed a significant effect of condition, $F(3,33) = 59.18$, $p < .001$, $\eta^2 = .84$ (Figure 4, below, top panel). Tukey HSD tests showed that RTs differed between each pair of deviation magnitudes by at least $p < .001$, except between 127-Hz and 320-Hz deviations.

ERP Measures

Visual inspection of the group-averaged deviant-minus-standard difference waveforms revealed two negative peaks in the 80–250-ms latency range for the 40- and 127-Hz deviations (Figure 2; Table 3). In these cases, the later peak, which coincided with the single difference peak on the corresponding deviant-minus-control difference waveform, was regarded as an estimate of MMN and the earlier one as a sign of an N1 difference. Group–averaged peak latencies are shown in Figure 4, below, top panel. The ANOVA of the individual peak latencies yielded a main effect of the magnitude of deviance, $F(3,33) = 35.29$, $\varepsilon = .72$, $p < .001$, $\eta^2 = .76$, and an interaction between derivation and deviance magnitude, $F(3,33) = 4.60$, $\varepsilon = .64$, $p < .05$, $\eta^2 = .29$ (Table 3, Figure 4, below, top panel). Tukey post hoc HSD tests showed that each increase of deviation was accompanied by a shortening of the difference peak latency with either derivation (by at least $p < .01$), except for the step between 40 and 127 Hz measured from the deviant-minus-control difference waveforms. Corresponding measures based on the two derivations did not significantly differ from each other, except at the largest (320 Hz) deviation, which showed a shorter latency with the deviant-minus-standard than with the deviant-minus-control derivation ($p < .05$), thus explaining the significant interaction.

Both types of difference waveforms showed fronto–central negativities with polarity reversal at the mastoids at all levels of deviance (Figure 3, Table 4). The ANOVA of the amplitude measures yielded a main effect of the magnitude of deviance, $F(3,33) = 4.40$, $\varepsilon = .68$, $p < .05$, $\eta^2 = .29$, and an interaction between derivation and deviance magnitude, $F(3,33) = 6.35$, $\varepsilon = .64$, $p < .01$, $\eta^2 = .37$ (Figure 4, bottom panel). Tukey post

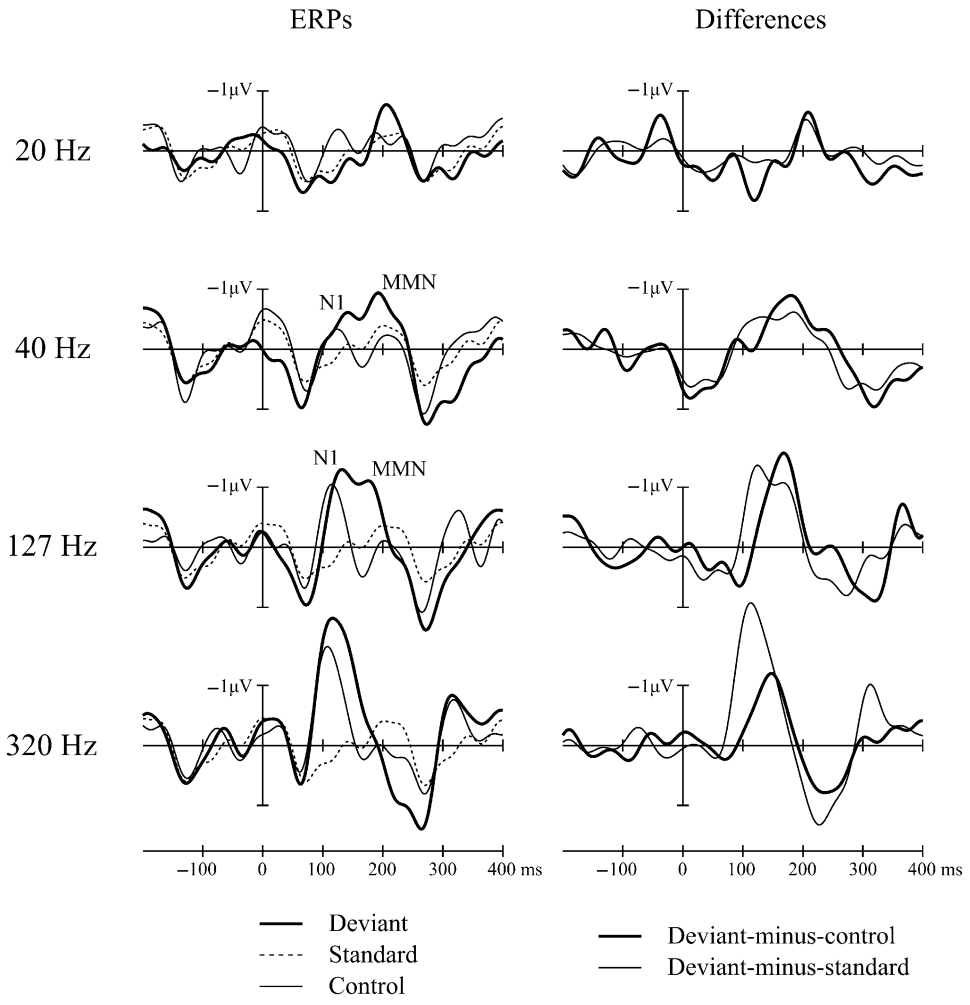

Figure 2. Group-averaged deviant, standard, and control ERPs (left), and deviant-minus-standard and deviant-minus-control difference waveforms (right) at the Fz electrode for the four levels of the magnitude of deviance. For the 40- and 127-Hz magnitude of deviance conditions the N1 and MMN peaks are indicated on the deviant ERP waveform (left).

hoc HSD tests showed that the amplitude measure obtained with the deviant-minus-standard derivation at 320 Hz differed significantly from all other amplitude values except for that obtained with the deviant-minus-control derivation at 127-Hz deviation ($p < .01$ for all comparisons). Furthermore, the amplitude measured with the deviant-minus-control derivation at 127 Hz was significantly higher than that obtained at 20 Hz ($p < .05$ for the deviant-minus-standard, and $p = .054$ with the deviant-minus-control derivation), but not from the other amplitudes obtained with the deviant-minus-control derivation ($p > .37$ at least). For deviant-minus-standard comparisons, p values for nonsignificant effects were at least .51.

Table 3. *Group-Averaged Difference Waveform Peak Latencies (Where Applicable, Standard Errors are in Parentheses)*

	Peak latencies measured from the group-averaged difference waveforms (ms)		Group-averaged individual difference–waveform peak latencies (ms)	
Magnitude of deviance (Hz)	Deviant minus standard	Deviant minus control	Deviant minus standard	Deviant minus control
20	206	208	209 (5)	209 (7)
40	134/184	180	183 (8)	172 (9)
127	124/166	168	157 (8)	167 (4)
320	114	148	117 (5)	139 (7)

Discussion

Our results showed that deviance detection improved and became faster with increasing magnitudes of deviation up to the 127 Hz where it reached a close-to-perfect performance ceiling. In parallel, the peak latencies of the deviant-minus-standard and deviant-minus-control difference waveforms decreased, although this decrease was significantly larger at the largest (320 Hz) deviation for the deviant-minus-standard than for the deviant-minus-control derivation. The deviant-minus-standard difference amplitude increased with increasing magnitudes of deviation, whereas the same measure obtained with the deviant-minus-control derivation was not significantly affected by the magnitude of frequency deviation. Thus, in answer to our main question, we can state that the effect of the magnitude of deviance

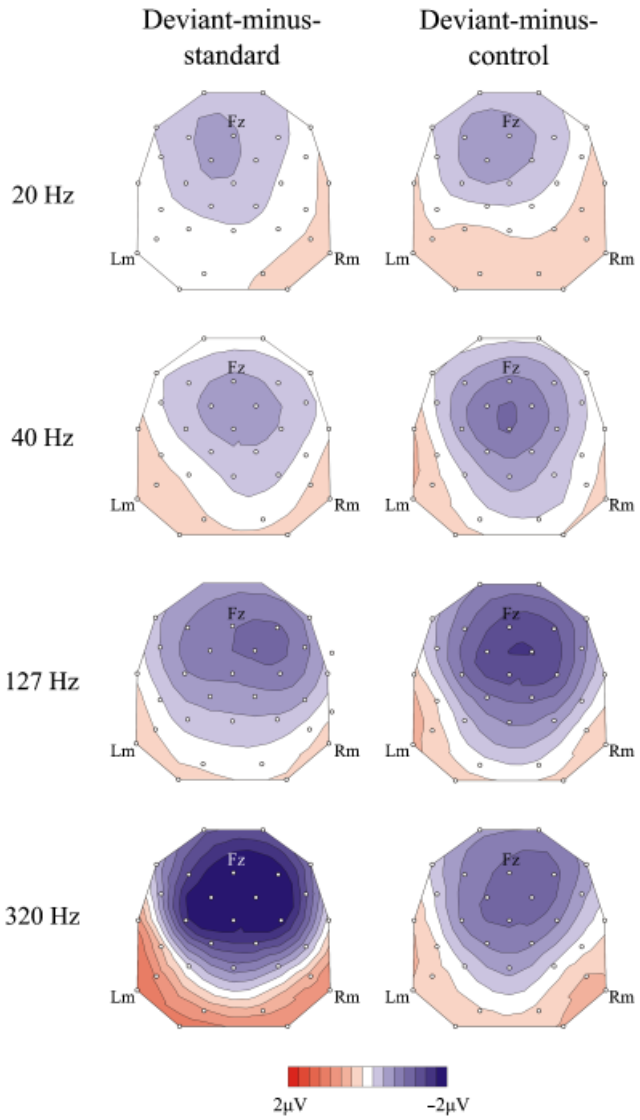

Figure 3. Topographical distributions of the group-averaged deviant-minus-standard and deviant-minus-control difference waveforms at the MMN peak latencies, separately for the four levels of the magnitude of deviance.

on the deviant-minus-standard difference amplitude is mainly (although not necessarily entirely) due to an effect on the N1 amplitude. Because the MMN peak latency is systematically affected by the magnitude of deviance, it is a more reliable correlate of the magnitude of deviance than the MMN amplitude, as has been previously suggested (Näätänen & Gaillard, 1983; Schröger & Winkler, 1995). Both our behavioral results and the ERP measures obtained with the deviant-minus-standard derivation replicated the corresponding results of Tiitinen and his colleagues (1994) with reasonable accuracy, although on average our subjects responded slower to deviants than the representative participant in the Tiitinen et al. study. Furthermore, choosing the earlier deviant-minus-standard peak at 40- and 127-Hz deviations would have resulted in an even closer correspondence between the current and Tiitinen et al.'s peak latency results.

The effects of the magnitude of stimulus change on the N1 amplitude come as no surprise given either one of the explanations offered for the N1 response decrement elicited by closely spaced sounds (Budd et al., 1998; Lü et al., 1992b; May et al., 1999; for a review, see Näätänen & Picton, 1987). However, the MMN results (a significant amplitude difference found between the responses elicited by the 20- and 127-Hz deviants only and a significant latency effect) require more thorough consideration. First, it is possible that the MMN amplitude increases modestly with the magnitude of frequency deviance, but the discriminative power of the current methods was insufficient to show this effect for each frequency increment. Supporting this assumption is the numerical increase in mean MMN amplitudes between 20- and 127-Hz deviations (Figure 3, Table 4). Some effect of the magnitude of stimulus deviance must be expected, because it is plausible to assume that as the magnitude of deviance approaches zero, the MMN amplitude should decrease. At least, when the difference between the standard and the deviant sound decreases below the sensitivity of the afferent system, then no MMN can be elicited. Given the probabilistic nature of discrimination close to threshold levels and the properties of the averaging method of estimating the MMN response, at near threshold levels, decreasing MMN amplitudes can be expected (Amenedo & Escera, 2000; Näätänen & Alho, 1997). However, we also found a numerical amplitude decrease between 127- and 320-Hz deviations (Figure 3, Table 4), which argues against the notion of a monotonic increase of the MMN amplitude as a function of the magnitude of deviation, at least at larger magnitudes of deviation.

Table 4. *Group-Averaged Difference Waveform Peak Amplitudes (Standard Errors are in Parentheses)*

Magnitude of deviance (Hz)	Deviant-minus-standard amplitude (μV)	Deviant-minus-control amplitude (μV)
20	– 0.48 (0.21)	– 0.58 (0.29)
40	– 0.60 (0.21)	– 0.87 (0.27)
127	– 1.05 (0.35)	– 1.51 (0.44)
320	– 2.31 (0.38)	– 1.16 (0.22)

The deviant-minus-control derivation may underestimate the MMN amplitude (Schröger, 1997b) due to the larger acoustic separation between the control and replacement than between the deviant and the standard tones (see the final paragraph of the introduction). Therefore, it is important to assess whether the results could have been systematically biased by this effect (i.e., by increased underestimation of the MMN amplitude with increasing magnitudes of deviance). Although there is no a priori argument against this possibility, internal consistency of the current results suggests that the possible underestimation of the MMN amplitude does not invalidate our conclusions. The deviant-minus-standard difference waveforms show separable N1 waves in the 40- and 127-Hz conditions (see Figure 2, left column). These N1 amplitudes closely corresponded to those obtained for the control tones presented in the corresponding control conditions, suggesting that in these conditions, the control procedure provided an accurate estimate of the N1 amplitude. Indeed, the MMN amplitudes obtained by the deviant-minus-control derivation were numerically very close to the estimates provided by the deviant-minus-standard derivation (see Figure 4, bottom, for the derived MMN amplitudes). Because no distinct N1 peak could be observed for the 320-Hz condition, the critical question is, therefore, whether or not the lack of MMN amplitude increase from 127- to 320-Hz deviation

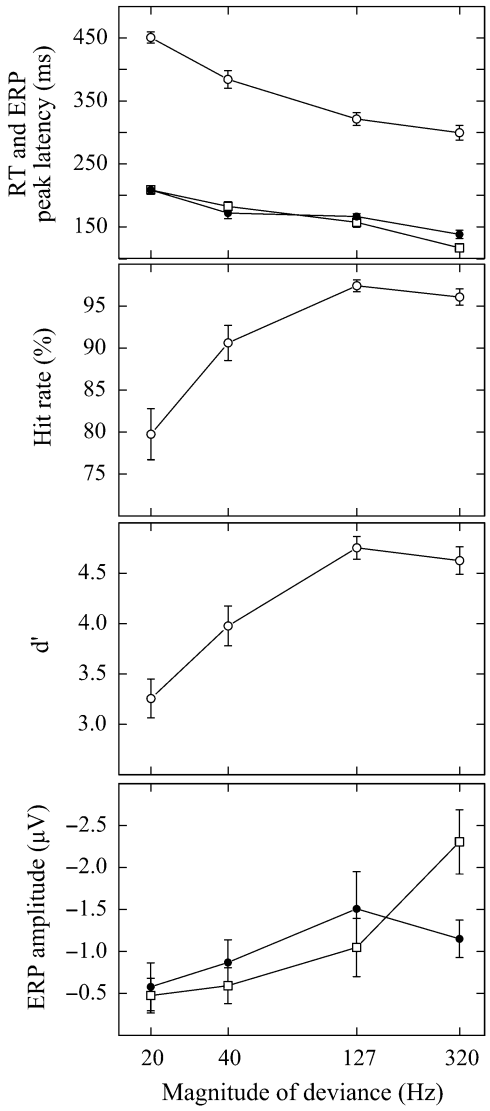

Figure 4. Summary of the group-averaged performance and ERP measurements as the function of the magnitude of deviance. The top panel shows the reaction times and MMN peak latencies (deviant-minus-standard and the deviant-minus-control derivations, separately), the second panel the hit rate, the third panel the d' values, and the bottom panel the MMN amplitudes obtained with the deviant-minus-standard and the deviant-minus-control derivations. Error bars denote standard errors of means.

was caused by an inflated N1 amplitude estimate in the 320-Hz control. Because the N1 amplitude elicited by a given sound increases (or at least does not decrease) with increasing acoustical separation between this sound and the other sounds delivered within the last ca. 15 s (Butler, 1968; Näätänen et al., 1988; for a review, see Näätänen & Picton, 1987), it is plausible to assume that the amplitude of the control N1 in the 320-Hz condition should be as high or higher than that in the 127-Hz condition (-1.04 μV peak amplitude at Fz). Thus if one accepts that (1) the control N1 estimate was accurate in the 127-Hz condition (because in this condition, the N1 peak could be separated and the measured amplitude was consistent across the two estimates) and (2) the N1 amplitude in the 320-Hz condition cannot be less than that in the 127-Hz condition, then the minimum of the N1 amplitude in the 320–Hz condition is 1.04 μV. By using this minimal N1 estimate, the shortening of MMN latency, which leads to a larger N1-MMN overlap, cannot result in an artificial reduction of the MMN estimate. Recalculating the MMN amplitude for the 320-Hz condition with this minimal N1 amplitude estimate (the control N1 peak measured in the 320-Hz condition [-1.65 μV] proportionally reduced to match the N1 peak amplitude measured in the 127-Hz condition—this procedure retains the effect of stimulus separation on the N1 peak latency; see Figure 5, left) results in an MMN peak amplitude estimate of -1.37 μV (see Figure 5, right). Because this estimate is still numerically lower than that obtained in the 127-Hz condition (deviant-minus-control derivation: -1.57 μV), it is unlikely that the lack of MMN amplitude increase between 127- and 320-Hz deviation was caused by overestimating the 320-Hz control N1 amplitude. The MMN amplitude estimate obtained by the deviant-minus-reduced-control derivation was significantly lower than that obtained with the deviant-minus-standard derivation in the 20-ms window centered on the peak latency of group–averaged waveforms, $t(11) = 2.75$, $p < .05$. Thus the minimal estimate of N1 led to (1) no MMN amplitude increase from 127- to 320-Hz deviation and (2) a significantly lower MMN amplitude estimate compared with the deviant-minus-standard difference derivation.

A reasonable account of the current MMN amplitude results suggests that the MMN amplitude is correlated with the probability of detecting a deviant. When a regularity violation is salient, all instances of the deviant elicit the MMN. When deviants are difficult to detect, MMN is elicited only on a fraction of deviant trials. Because MMN is estimated from the average of many trials, this leads to lower average MMN amplitudes being measured. This explanation covers all previously observed magnitude of deviance effects on the MMN amplitude, including those found, for example, for tone intensity (see Näätänen, 1992, pp. 139–143).

This account does not require, although neither is it incompatible with, the assumption that the magnitude of deviance affects the amplitude of the MMN responses elicited on individual instances of deviance. The alternative assumption is that MMN is elicited in an all-or-none fashion on each trial, and any effect of the magnitude of deviance is mediated by the discriminability of the deviant from the standard (for similar suggestions, see Winkler, Reinikainen, & Näätänen, 1993; Woods, 1990). That is, the MMN amplitude is determined by the ratio of detected and undetected instances of the deviation. If this were true, gradual MMN amplitude increase with increasing magnitudes of deviance may only be found for near threshold deviations, and then the MMN amplitude should strongly correlate with detection performance (see Näätänen & Alho, 1997). The present results are compatible with this account of the MMN amplitude measure. Because the magnitudes of deviance used in the present study were above the just noticeable difference, detection performance was quite high, with hit rates between ca. 80% and 98% (see Table 2). Thus we can assume that MMN has been elicited on ca. 80% of the deviant trials at the lowest (20 Hz) level of deviation as opposed to the ca. 96%–97% at the highest levels of deviation (127 and 320 Hz). The nonsignificant numerical MMN amplitude increase found between these magnitudes of deviation may reflect the proportionally small increase

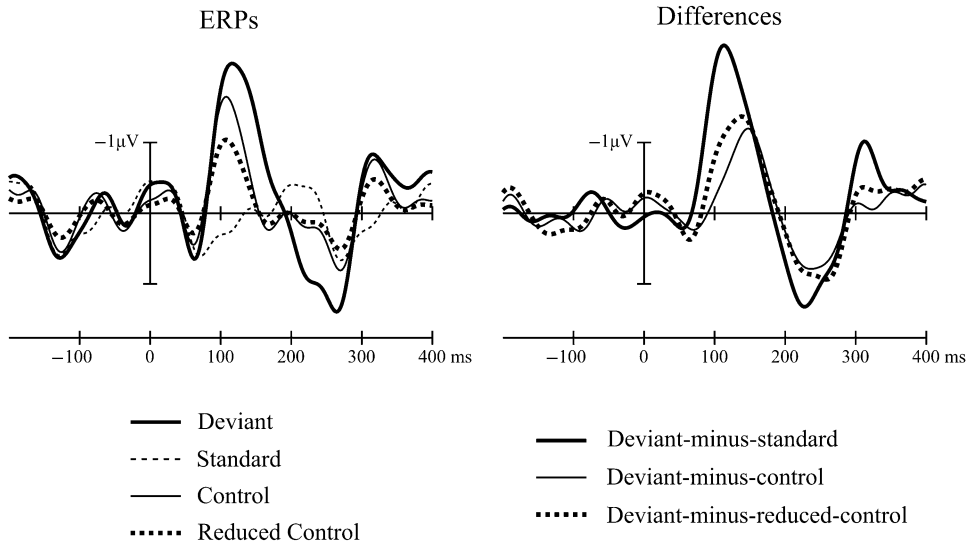

Figure 5. Group-averaged deviant, standard, control, and 63% reduced control ERPs, (left), together with deviant-minus-standard, deviant-minus-control, and deviant-minus-reduced-control difference waveforms (right) at Fz for the 320-Hz magnitude of deviance condition. The N1 wave in the reduced control ERP has the same peak amplitude as the 127-Hz control N1 (− 1.04 μV) while retaining the temporal properties of the N1 elicited in the 320-Hz condition. The deviant-minus-reduced-control MMN amplitude estimate is lower than the peak amplitude of the 127-Hz deviant-minus-control MMN estimate (− 1.37 μV vs. − 1.57 μV).

of detection performance, whereas further increasing the magnitude of deviance did not result in a significant increase of the MMN amplitude.

Our observations of a magnitude of deviance effect on the N1 but not on the MMN amplitude is fully compatible with Rinne et al. (2006) and Campbell et al.'s (2007) conclusions that auditory distraction and memory disruption are related to the N1 but not to the MMN response (but see Muller-Gass et al., in press). However, our results do not support the notion of the role of MMN in initiating an attention switch to the deviant stimulus. Although it is still possible that the MMN signal may be involved in the direction of attention, the arguments that larger deviations result in higher MMN amplitudes, which in turn are more likely to be followed by P3a and a switch of attention, has now been questioned by the present results as well as those of Rinne at al. (2006) and Campbell et al. (2007). What could then be the primary function of the MMN-generating process? An alternative hypothesis of the role of the MMN-generating process suggests that it is involved in adjusting the representation of those regularities, whose prediction was violated by the deviant sound (Winkler, in press; Winkler & Czigler, 1998; Winkler et al., 1996; Winkler, Schröger, & Cowan, 2001). The magnitude of deviation does not necessarily play a role in this process. Winkler (in press) suggested that the MMN–generating process decreases the weight (reliability) carried by subsequent predictions of the given regularity. This weight is not related to the amount of detected deviation, because smaller deviations do not make it more likely than larger deviations that the prediction will be correct next time. Another result supporting this notion is that in a roving–standard paradigm, in which the standard stimulus changes from stimulus train to stimulus train, forcing a new regularity representation to be formed for each train, MMNs of uniform amplitude were elicited with three or more standard sounds preceding the deviant, but there was no MMN when the deviant was preceded by less than three standards (Cowan et al., 1993; cf. Bendixen, Roeber, & Schröger, in press; although Haenschel, Vernon, Dwivedi, Gruzelier, and Baldeweg, 2005, found an increase in the deviant-minus-standard differences with increasing number of preceding standard sounds, this was due to the amplitude increase of a component termed "repetition positivity" elicited by the standard stimuli, whereas the deviant–stimulus response remained constant; for a review, see Baldeweg, 2006). Cowan et al.'s result suggests that MMN does not reflect the number of the stimuli forming neural representations involved in the MMN-generating process. Rather, MMN reflects the existence of a representation of stimulus repetition. Violating this regularity is not dependent on the amount of deviation (beyond the detectable amount of deviance) and, therefore, the MMN amplitude would not reflect the amount of perceived difference between the standard and the deviant sound.

In summary, the present results show that for clearly discriminable deviations, the MMN amplitude does not depend on magnitude of deviance. However, for near threshold deviations, the MMN amplitude may reflect the rate of deviance detection: The average MMN amplitude increases with the detection ratio. However, when detection performance approaches the ceiling level, increasing the magnitude of change will cause no or only a very small increase of the MMN amplitude.

These conclusions have two important implications for studies utilizing MMN for measuring auditory discrimination abilities. (1) The experiments should use a control procedure that limits the influence of N1-related effects on the results, especially when discrimination performance is close to being perfect. (2) MMN can still be used as a measure of the accuracy (or "resolution") of the auditory system, because such investigations by definition will test near threshold amounts of deviation. Finally, recent converging evidence questions the role of MMN in passive attention, suggesting that the primary function of the MMN–generating process lies in maintaining the neural representation of the auditory environment.

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