

The Role of Large-Scale Memory Organization in the Mismatch Negativity Event-Related Brain Potential

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Abstract

■ The mismatch negativity (MMN) component of event-related brain potentials is elicited by infrequent changes in regular acoustic sequences even if the participant is not actively listening to the sound sequence. Therefore, the MMN is assumed to result from a preattentive process in which an incoming sound is checked against the automatically detected regularities of the auditory sequence and is found to violate them. For example, presenting a discriminably different (deviant) sound within the sequence of a repetitive (standard) sound elicits the MMN. In the present article, we tested whether the memory organization of the auditory sequence can affect the preattentive change detection indexed by the MMN. In Experiment 1, trains of six standard tones were presented with a short, 0.5-sec stimulus onset asynchrony (SOA) between tones in the train. This was followed by a variable SOA between the last standard and the deviant tone (the “irregular presentation” condition). Of 12 participants displaying an MMN at the 0.5-sec predeviant SOA, it was

elicited by 11 with the 2-sec predeviant SOA, in 5 participants with the 7-sec SOA, and in none with the 10-sec SOA. In Experiment 2, we repeated the 7-sec irregular predeviant SOA condition, along with a “regular presentation” condition in which the SOA between any two tones was 7 sec. MMN was elicited in about half of the participants (9 out of 16) in the irregular presentation condition, whereas in the regular presentation condition, MMN was elicited in all participants. These results cannot be explained on the basis of memory-strength decay but can be interpreted in terms of automatic, auditory preperceptual grouping principles. In the irregular presentation condition, the close grouping of standards may cause them to become irrelevant to the mismatch process when the deviant tone is presented after a long silent break. Because the MMN indexes preattentive auditory processing, the present results provide evidence that large-scale preperceptual organization of auditory events occurs despite attention being directed away from the auditory stimuli. ■

INTRODUCTION

The mismatch negativity (MMN) component of event-related brain potentials (Näätänen, Gaillard, & Mäntysalo, 1978; for recent reviews, see, Näätänen & Tiitinen, 1998; Schröger, 1997; Ritter, Deacon, Gomes, Javitt, & Vaughan, 1995) has become an important tool in understanding the functioning of the brain in auditory perception and immediate memory. The MMN is a frontocentrally negative ERP component that is obtained when a sound violates some preattentively detected regularity of the auditory stimulus sequence. For example, when a repeating sound or simple pattern of sounds, termed the “standard,” infrequently changes in a discriminable manner to become “deviant,” MMN is elicited even if the experimental participant is absorbed in a different task and no responses to the sounds are required (e.g., Sams, Paavilainen, Alho, & Näätänen, 1985; see further, Schröger, 1997; Näätänen, 1992). Näätänen (1984, 1985, 1990) proposed that MMN is elicited as a consequence of the deviant mismatching

an auditory sensory memory of the repetitive standard. Cowan, Winkler, Teder, and Näätänen (1993) found no MMN when the repetitive standard stimuli were separated from the deviant by 11–15 sec, whereas Sams, Hari, Rif, and Knuutila (1993) obtained an MMN in only half of their subjects with a 12-sec regular ISI. Therefore, after about 12 sec, it has been assumed that the sensory memory record of the standard stimulus has faded, leaving no basis on which a discrepancy between the standard and deviant sound could be detected. The MMN thus offers a way to learn about processes of auditory discrimination and memory that do not depend on the active, willful involvement of the participant.

Recent investigations (Ritter, Gomes, Cowan, Sussman, & Vaughan, 1998; Winkler, Karmos, & Näätänen, 1996; Winkler & Czigler, 1998; Cowan et al., 1993) have suggested that the memory directly involved in the MMN-generating process contains “records of the preattentively detected regularities of the auditory stimulus sequence” (e.g., the repetition of a tone, the alternation of two tones, some periodicity of the sound sequence, etc.) rather than just an “auditory sensory memory” record of the repetitive standard sound itself. This notion is also supported by results showing that MMN

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can be elicited by violating such regularities that do not involve stimulus repetition. In such cases, no simple sensory memory trace could suffice for determining whether or not a given sound mismatches the preceding auditory stimulus sequence. For example, MMN was obtained for infrequent stimulus repetitions appearing within trains of tones with continuously increasing or decreasing frequencies (Tervaniemi, Maury, & Näätänen, 1994; see also Saarinen, Paavilainen, Schröger, Tervaniemi, & Näätänen, 1992 for another example of MMN being elicited without a repetitive standard stimulus). The difference between the two assumptions about the contents of the memory underlying the MMN-generating process (i.e., regularity vs. sensory memory trace) becomes critical when MMN is employed for measuring the duration of auditory sensory memory. If the discriminative mismatch process required only an auditory sensory memory trace of the repetitive standard sound, then the lack of MMN at long predeviant intervals implies a corresponding absence of the standard-stimulus memory trace. In contrast, according to the regularity–memory assumption, the presence of an auditory sensory memory trace of the repetitive standard stimulus is not a sufficient memory prerequisite of MMN elicitation. That is, even if the sensory memory record of the standard sound is present in the auditory sensory memory system, variables affecting the preattentive detection of regularities within the auditory input, the maintenance versus decay of regularity records, or the applicability of a regularity rule to a given auditory stimulus may prevent the elicitation of the MMN.

The dependence of the MMN on the time between the standards and deviant has been studied using simple stimulus series in which the standard is a single repeating tone and the deviant is a different tone. Some studies tested the elicitation of MMN at different intertone intervals in constant-ISI sequences (i.e., the interval preceding the deviant stimulus was equal to that separating consecutive standards, which we term *regular presentation*; Jääskeläinen, Hautmäki, Näätänen, & Ilmoniemi, 1999; Grau, Escera, Yago, & Polo, 1998; Schröger & Winkler, 1995; Imada, Hari, Loveless, McEvoy, & Sams, 1993; Sams et al., 1993; Czigler, Csibra, & Csontos, 1992; Mäntysalo & Näätänen, 1987; Näätänen, Paavilainen, Alho, Reinikainen, & Sams, 1987). One problem with regular presentation is that the separation in time between the standard tone series and the deviant tone is fully confounded with the separation between standard tones. Because the cumulative strength of the sensory memory representation of the standard may depend upon the time between standards, the loss of MMN (or a possible decrease of the MMN amplitude) as a function of the time between tones in this procedure cannot be taken as an estimate of the rate of forgetting of the sensory memory of the standard tone sequence. This problem can be addressed using various procedures in which the durations of silent intervals between tones are

mixed within a session (Böttcher-Gandor & Ullsperger, 1992). One way to avoid the confounding introduced by regular stimulus presentation is to use a relatively rapid train of standard tones grouped together and followed by a longer, variable silent interval before the deviant tone (which we call “irregular” presentation). This technique was employed by several studies (Gomes et al., 1999; Jääskeläinen et al., 1999; Grau et al., 1998; Ritter et al., 1998; Cowan et al., 1993). However, this introduces another potential problem. The organization of tones in memory over a long time scale could be influenced by the pattern of standard and deviant tone presentation. We term this organization *preperceptual* to acknowledge that, although it probably influences perceptual organization as indicated in behavioral responding, there could be differences between the two forms of organization. This large-scale preperceptual organization could affect the type of regularities extracted from the sound sequence, which could then play a role in the elicitation of the MMN component. It is this possibility that we investigate in the present article.

A recent behavioral study illustrates that if one does not take perceptual organization into account, one may obtain a spurious estimate of the decay of auditory sensory memory over time. Cowan, Saults, and Nugent (1997) reexamined the simple paradigm in which two slightly different tones are presented on a trial, separated by a variable silent interval, and the participant is to indicate whether the second tone is higher or lower in pitch than the first tone. Performance in this type of procedure typically declines as the interval between tones is increased to about 10 sec. It has been assumed that this decline reflects the decay of sensory memory for the first tone in a pair. However, Cowan et al. brought up the possibility that perceptual grouping could play a role even in this simple task. In particular, in studies of this sort, there is generally about 4 or 5 sec between trials. When the two tones to be compared are separated by more than this, the first tone in a pair is temporally closer to the second tone of the previous trial than it is to the tone with which it is supposed to be compared. Many studies have suggested that there is a tendency to group tones together perceptually (or conceptually) when they occur relatively close together in time (Bregman, 1990). To control for this factor, Cowan et al. (1997) varied not only the time between tones to be compared, but also the time between trials. It was found that some of the alleged sensory memory decay effect actually should be attributed to the ratio between the intertrial interval and the following intratrial (intertone) interval; performance levels were higher when the intertrial interval was relatively large. However, some forgetting still occurred as a function of the intratrial interval even with the ratio between the two intervals controlled. Thus, both the grouping effect and sensory memory decay appeared to play a role in tone comparison performance. There are various other behavioral studies also suggesting that

perceptual organization takes place over a long period of time (Beauvois & Meddis, 1997; Anstis & Saida, 1985; Bregman, 1978, 1990).

In MMN experiments, it must be considered that an MMN could fail to occur at long standard-deviant temporal separations not because sensory memory of the standard has faded, or at least not totally because of that factor; but at least partially because preperceptual grouping may separate the deviant from the standard stimuli (i.e., place them in separate groups). One cannot be sure whether grouping in memory can affect the mismatch process because we do not know to what extent such grouping depends on deliberate, willful attention to sounds. However, one recent MMN study, where attention was directed away from the sounds, indicates that preperceptual grouping of sounds can occur without willful attention. In particular, Sussman, Ritter, and Vaughan (1999) presented alternating sequences of low and high tones, with three tones in each range. Separately, both low and high tones formed repetitive patterns of increasing tone frequency (i.e., low-1, low-2, low-3 interleaved with high-1, high-2, and high-3). When the tones were presented at a relatively slow pace, the repeating patterns were obscured in perception by the overall alternation between low and high tones. Consequently, infrequent deviant patterns (low-3, low-2, low-1 or high-3, high-2, high-1) did not elicit the MMN. However, when the rate of stimulus presentation was increased to a pace where separate low and high sound streams emerged in perception, the repetitive tonal patterns could be easily detected and MMN was elicited by the infrequent deviant patterns. As Sussman et al.'s experimental participants were reading a book and ignoring the auditory stimuli, it seems possible that some types of grouping in memory occur preattentively and thus could affect the MMN-generating process.

In the present article, we use the concepts of memory decay and preperceptual grouping to identify the basis of individual differences in MMN elicitation at relatively long predeviant intervals. Experiment 1 was performed to find within the irregular presentation paradigm a predeviant interval at which tone-duration deviants do not anymore elicit an MMN in all participants. Thus Experiment 1 used the typical irregular presentation design (like in Cowan et al., 1993) with two additions, which have not been done in previous studies using this paradigm: (a) ERP responses were carefully checked in order to identify different individual response patterns and (b) the possibility that the maximal predeviant interval after which MMN is still elicited depends on the amount of stimulus deviation (both on the group and individual levels) was also tested. In Experiment 2, we tested whether individual differences in the large-scale organization of a sound sequence could account for at least some of the interindividual variability in the MMN elicitation observed in Experiment 1. This was done by comparing the responses to the tone-duration

deviants following the critical predeviant interval (from Experiment 1) in the regular versus irregular presentation paradigms.

EXPERIMENT 1

Experiment 1 used an irregular presentation paradigm in which each train of standard tones was presented at a relatively fast rate and was followed by a longer, variable silent interval before the deviant stimulus. Trains consisted of six identical standard tones separated by a 0.5-sec SOA, and a final, "deviant/control" tone separated from the last of the six standards by an SOA of 0.5, 2.0, 7.0, or 10.0 sec. The deviant/control tone was always 100 msec long. Depending on the experimental condition, the preceding six tones (the standards) were all 100 msec (in the control condition), 170 msec (small deviance condition), or 300 msec (large deviance condition) long. Because the difference between the deviant tone and either one of the standard tones commences at the offset of the 100-msec-long deviant tone, the MMN component is expected to appear between 200 and 300 msec from the onset of the deviant tone.

Results

The data from three experimental participants had to be rejected from the analysis, two due to the presence of extensive artifacts, one because none of the present conditions elicited an observable MMN in that participant.

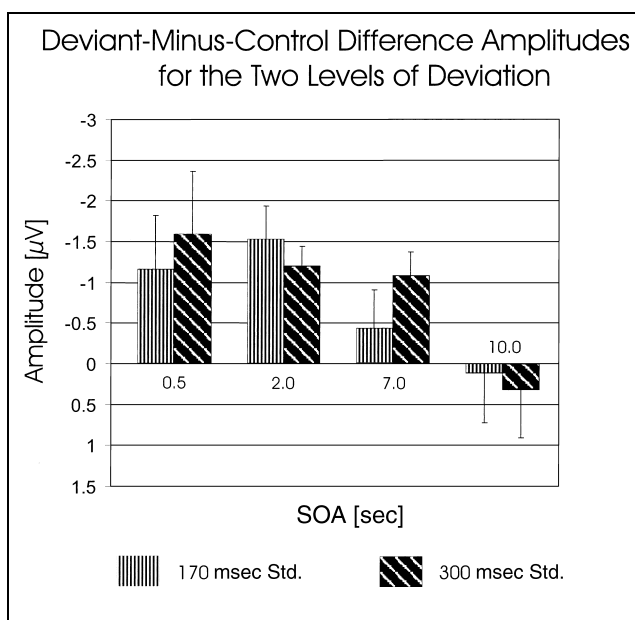


Figure 1. Experiment 1. Grand-average Fz deviant-minus-control difference-wave amplitudes at different predeviant SOAs and magnitudes of stimulus deviation (i.e., standard-stimulus durations). (See the measuring algorithm in Methods and the measurement intervals in Table 1.) Standard errors of mean (S.E.M.) are displayed on top of each bar.

MMN responses

Figure 1 shows the frontal (Fz) deviant-minus-control difference-wave amplitudes (see the measuring algorithm in Methods) at each predeviant SOA and magnitude of stimulus deviation, averaged from the responses of all experimental participants. The corresponding ANOVA test on deviant-minus-control difference-wave areas (SOA \times magnitude of deviation) showed no significant effect; the negative difference, however, tended to decrease with increasing predeviant SOAs [$F(3, 33) = 2.84, p < .07$, Huynh–Feldt $\epsilon = 0.8575$]. No difference was found by dependent t tests between the difference-wave amplitudes elicited by the two magnitudes of stimulus deviation at any SOA.

The lack of a significant SOA effect despite the visually clear change of the deviant-minus-control difference-wave amplitude (Figure 1) suggested that individually different patterns of results might be obscured within the grand-average curves. In the individual experimental participants' responses, three markedly different response patterns could be discerned. One experimental participant elicited a large MMN component at the 0.5-sec SOA, but no MMN at any of the longer SOAs. Six experimental participants (short-SOA group) elicited sizable MMN responses at 0.5- and 2-sec SOAs, but no MMN at longer SOAs. Finally, five experimental participants (long-SOA group) elicited clear MMN responses at 0.5, 2, and 7 sec, but no MMN at 10 sec. No MMN was elicited by any of the experimental participants at 10 sec.

Based on the above assessment of the responses of individual experimental participants, the MMN peak latencies elicited by the two magnitudes of stimulus deviation were compared at the 0.5-, 2- and 7-sec SOAs (only for those experimental participants who elicited a

Table 1. Experiment 1. Fz Deviant-Minus-Control Peak, 50% Peak Amplitude (Measurement Start and End) Latencies (in msec From the Stimulus Onset), and Grand Average (Across All Subjects) Deviant-Minus-Control Difference-Wave Amplitudes (in $\mu\text{V} \pm$ Standard Error of Mean) of Possible MMN Responses at the Different SOAs (Collapsed Across the Two Levels of Deviations)

SOA [sec]	Start	Peak	End	Amplitude
0.5	208	252	288	-1.37 ± 0.68^a
2.0	228	268	288	-1.30 ± 0.31^b
7.0	228	240	268	-0.75 ± 0.28^a
10.0	260	272	284	0.21 ± 0.47

The marked significance levels were obtained by one-sided dependent t tests between the deviant and control response amplitudes in the given measurement ranges.

$df = 11$.

^a $p < .05$.

^b $p < .01$.

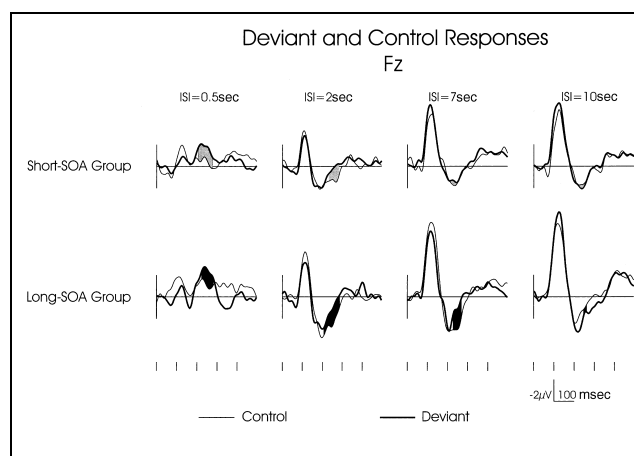


Figure 2. Experiment 1. Responses to deviant and control stimuli at different predeviant SOAs in the short-SOA and long-SOA groups. The areas measured (see Methods and Table 2) are filled gray (short-SOA group) or black (long-SOA group).

negative deviant-minus-control difference wave in the 200–300 msec range at the given SOA). Dependent t tests showed no significant difference between the two magnitudes of stimulus deviation at any of these SOAs. The lack of a significant MMN area (see above) or latency effect as a function of the magnitude of stimulus deviation variable enabled us to eliminate this factor from the remaining analyses. Therefore, to reduce the noise that remained in the responses due to the relatively small numbers of repetitions for separate sequence types (which was practically inevitable given how long each train took to present), the responses to the identical

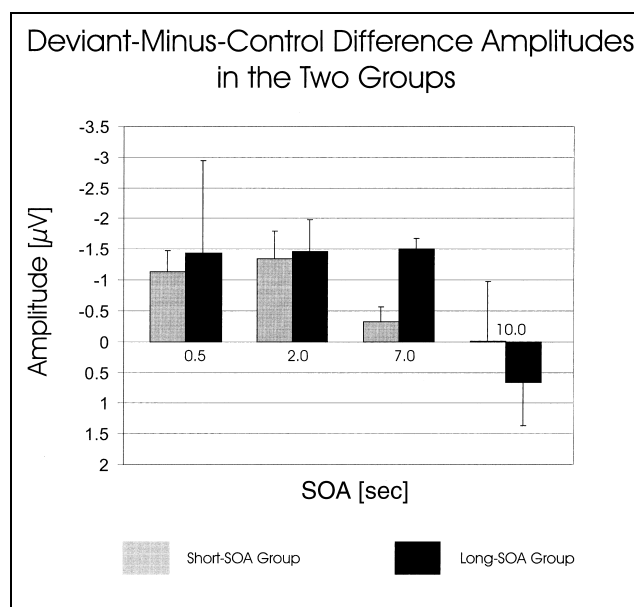


Figure 3. Experiment 1. Fz group-average deviant-minus-control difference-wave amplitudes at different SOAs for the short-SOA and long-SOA groups. (See the measuring algorithm in Methods and the measurement intervals in Table 2.) Standard errors of mean (S.E.M.) are displayed on top of each bar.

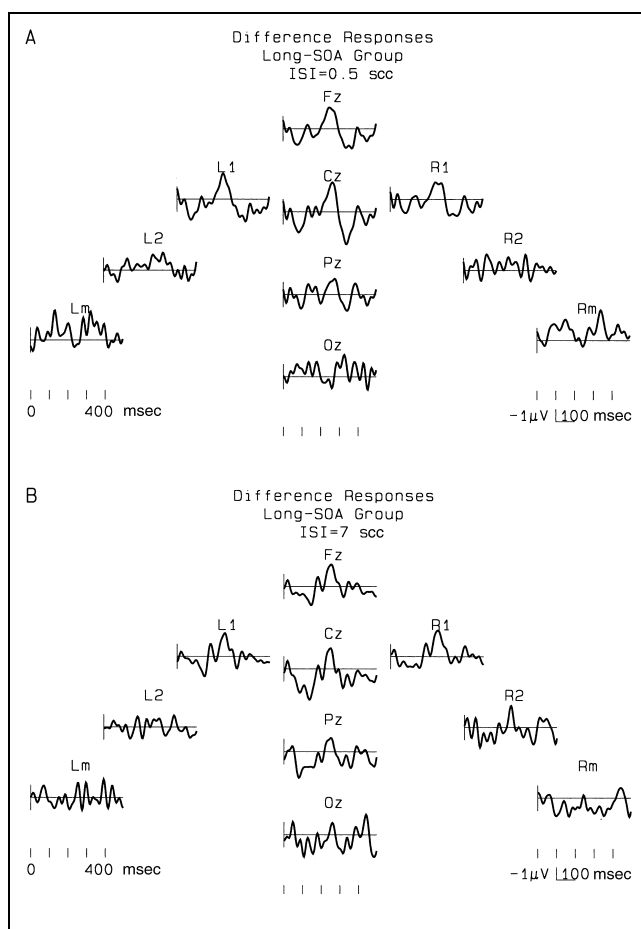


Figure 4. Experiment 1. Deviant-minus-control difference curves from all recording locations for the long-SOA group at 0.5 (A) and 7 sec (B).

deviants following the two different standards were collapsed in the following analyses.

The elicitation of the MMN component was tested separately at each predeviant SOA by one-sided dependent *t* tests between the Fz deviant and control responses. Significant negative deviant versus control differences were found at 0.5-, 2-, and 7-sec predeviant SOAs (Table 1).

In the following analyses, responses of the short-SOA and long-SOA groups are compared. (This comparison includes 11 participants in whom MMN was elicited at

the 2.0-sec SOA and excludes the one in whom MMN was elicited only at the shortest, 0.5-sec SOA.) Figure 2 presents the averaged responses to deviant and control stimuli at each SOA in the two groups. The corresponding difference-wave amplitudes are shown by Figure 3. The scalp distribution of the deviant-minus-control differences (shown for the 0.5- and 7-sec SOAs in the long-SOA group by Figure 4) is compatible with the notion that the negative difference waves observed in the 200- to 300-msec interval are in fact MMN components. An ANOVA test of the deviant-minus-control difference-wave areas (group \times SOA) revealed a significant SOA effect [$F(3, 27) = 4.25, p < .05, \epsilon = 0.5473$; see Table 2]. Tukey-type pairwise post hoc comparisons showed significant differences in the deviant-minus-control difference-wave areas between the 0.5 and 10 sec [$t(4, 27) = 4.21, p < .05$] and the 2- and 10-sec SOA pairs [$t(4, 27) = 4.71, p < .05$]. Comparison of the deviant-minus-control difference-wave areas between the two groups by two-sample *t* tests showed a significant difference only at the 7-sec SOA [$t(9) = 6.81, p < .001$] where the long-SOA group elicited a significant MMN response [$t(4) = 8.44, p < .01$] whereas the short-SOA group did not. This is of course a consequence of the selection of the two groups. The point of the above analysis is to demonstrate that the main locus of individual differences in MMN was at the 7-sec SOA.

N1 responses

N1 amplitudes were measured in the 104- to 124-msec postinterval because all N1 waves peaked between 108 and 120 msec from the stimulus onset. Varying the length of the interval preceding the deviant/control stimuli could be expected to affect the N1 amplitude elicited by these stimuli (see Näätänen & Picton, 1987). N1 amplitudes were measured to verify the presence of this well-known effect in our data. Indeed, the N1 amplitudes elicited by the deviant/control stimuli increased with increasing SOAs (see Figure 2). An ANOVA test of the central (Cz) N1 areas (group \times SOA \times preceding standard, 100/170/300 msec) showed a significant effect only for the SOA factor [$F(3, 27) = 34.48, p$

Table 2. Experiment 1. Fz Deviant-Minus-Control Peak, 50% Peak Amplitude (Measurement Start and End) Latencies (in msec From the Stimulus Onset), and Average Deviant-Minus-Control Difference-Wave Amplitudes (in $\mu\text{V} \pm \text{S.E.M.}$) of Possible MMN Responses in the Short-SOA and Long-SOA Groups (See Results) at the Different SOAs (Collapsed Across the Two Levels of Deviations)

SOA [sec]	Short group				Long group			
	Start	Peak	End	Amplitude	Start	Peak	End	Amplitude
0.5	204	216	280	-1.13 ± 0.35	228	248	284	-1.44 ± 1.50
2.0	232	272	284	-1.35 ± 0.44	208	252	288	-1.47 ± 0.51
7.0	220	228	240	-0.33 ± 0.23	228	256	272	-1.50 ± 0.18
10.0	212	216	220	-0.01 ± 0.97	244	256	268	0.67 ± 0.70

< .0001, $\epsilon = 0.6073$]. No other main effect or interaction reached the level of significance.

Discussion

At a first glance, the decrease of the MMN amplitude visible in Experiment 1 when the predeviant interval is prolonged to 7 or 10 sec seems to suggest that a gradual decay of the underlying sensory memory trace has prevented the elicitation of a full-amplitude MMN. However, this effect turned out to result from averaging: We found that individuals differed in whether or not they elicited an MMN at the 7-sec (and some even at the 2-sec) SOA between the closely grouped standard tones and the deviant tone. Furthermore, no gradual decrease of the MMN amplitude was shown in either group with increasing predeviant SOAs; the MMNs obtained at different SOAs had approximately equal amplitudes as long as MMN was elicited at all. This pattern of results suggests that the decay of the sensory memory trace of the standard might not be the only effect reflected by the present MMN measure. Thus the question arises as to what would occur if the standard tones were not grouped together (which we term an “irregular” presentation) but were spaced out, with a constant 7-sec interval between all tones in the series (which we term a “regular” presentation). This question is all the more important as, due to its shorter duration, the irregular-presentation paradigm used in Experiment 1 is more and more often used to assess the duration of auditory sensory memory in various developmental and patient groups (e.g., Grau et al., 1998).

Opposing predictions can be formed. First, theories of auditory sensory memory traditionally view the memory representation as decaying steadily across a 10- to 30-sec period (for a review see Cowan, 1995). According to this traditional view, the representation of the standard tone should be cumulative, depending simultaneously at any moment upon separate representations of all recent standard tones whose sensory memory traces have not yet decayed. The overall standard tone representation therefore should be stronger when the standard tones are grouped together into a rapid train, as in the irregular condition of Experiment 1, than when standard tones are separated by periods of 7 sec in a regular-presentation condition. Consequently, in those participants in whom no MMN is elicited in the irregular condition, neither should an MMN be elicited in the regular condition using the same predeviant interval. Furthermore, in some participants in whom MMN was elicited in the irregular condition, deviants following the same SOA might not elicit an MMN in the corresponding regular condition.

On the basis of preperceptual grouping, the prediction is the opposite. Tones in the regular condition may be coded in the brain as one steady, long series. In contrast, tones in the irregular condition may be coded in temporally defined groups, which could place the standards in a

different preperceptual group than the following deviant, this deviant being separated from the preceding closely spaced standard train by 7 sec. The key assumption is that the MMN depends on the standard tones and the following deviant being coded, or automatically organized, as belonging to the same group. In this case, even if no MMN was elicited in a given participant in the irregular condition (because the deviant was encoded in a separate preperceptual group from the preceding standard-stimulus train), deviants may still elicit the MMN in the corresponding regular condition. Furthermore, in all participants in whom MMN was elicited in the irregular condition, an MMN also should be elicited by deviants following the same predeviant interval in the regular condition. Both of these predictions are based on the assumption that the regular condition does not preperceptually separate the deviant from the preceding group of standards.

One reason why grouping could be important for the elicitation of the MMN component is that it might influence implicit (unconscious) expectations or sensory inferences, based on a neural model of the auditory environment. Winkler, Karmos, et al. (1996) suggested that this neural model contains records of the regularities preattentively extracted from the auditory input and that MMN is elicited by sounds violating the implicit expectations deriving from the model. It is quite possible that such implicit expectations are based on the model of each group of tones, separately (with groups defined as tones separated by a sufficiently short SOA), whereas there might be no implicit expectations bridging long gaps between groups.

EXPERIMENT 2

Experiment 2 tested the above question by comparing the elicitation of the MMN between the regular (constant 7-sec SOA between all tones of the train) and irregular (0.5-sec SOA separating the standard sound of the train, 7-sec predeviant SOA) modes of stimulus presentation. Test trains consisted of three standard tones (each 100 or 300 msec long) followed by a deviant/control tone (300 or 100 msec long). All other stimulus parameters were kept constant.

Results

Two experimental participants' data were rejected from the analyses due to extensive artifacts, another two because of very small numbers of artifact-free trials in either condition.

MMN responses

Experimental participants were divided into two groups on the basis of MMN elicitation in the irregular condi-

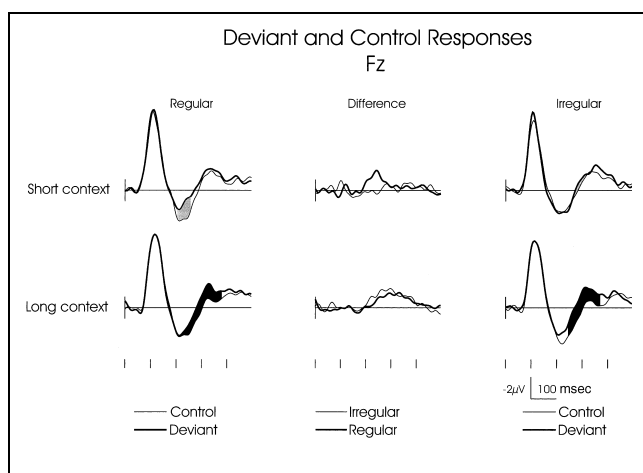


Figure 5. Experiment 2. Responses to deviant and control stimuli in the regular (left column) and irregular (right column) conditions for the short-context and long-context group. The corresponding difference curves are overlapped at the middle column. The areas measured (see Methods and Table 3) are filled gray (short-context group) or black (long-context group).

tion. Seven experimental participants, who showed no MMN in the irregular condition, were designated the “short-context” group. In nine experimental participants, MMN was elicited in the irregular condition (“long-context” group).

Figure 5 shows the group-averaged Fz responses to deviant and control stimuli obtained in the two conditions. The amplitudes of the corresponding deviant-minus-control difference waves are displayed in Figure 6 (peak and measurement latencies and mean amplitudes are given by Table 3). Scalp distributions of the deviant-minus-control differences elicited by the two groups in the regular condition are shown by Figure 7. The presence of MMN was tested by one-sided dependent t tests separately for each group and condition (Table 3). Significant deviant-minus-control differences were found in the regular condition for both groups and in the irregular condition for the long-context group only. (The latter result confirmed our group selection.) No difference was found between the MMN areas obtained in the regular versus irregular presentation conditions for the long-context group, whereas a significant difference was found between the corresponding measures for the short-context group by dependent t tests [$t(6) = 2.89, p < .05$]. The MMN peak latencies elicited in the two conditions did not significantly differ in the long-context group (276 ± 7.1 and 262 ± 11.6 msec for the regular and irregular conditions, respectively).

There was a significant interaction between the group and condition factors in the ANOVA of deviant-minus-control difference-wave areas [$F(1, 14) = 7.08, p < .05$]. The group difference was also significant [$F(1, 14) = 7.03, p < .05$]. Both of these effects were caused by the lack of MMN in the irregular condition in the short-context group. The MMN peak latency in the regular condition

was significantly shorter in the short-context than the long-context group (229 ± 7.7 and 276 ± 7.1 msec in the short-context and long-context groups, respectively; two-sample t test: $t(1, 14) = 4.38, p < .01$; see Figure 5).

N1 responses

N1 amplitudes were measured from the 100- to 120-msec poststimulus interval because all N1 waves peaked between 104 and 116 msec from the stimulus onset. An ANOVA test of the Cz N1 areas (group \times condition) showed that deviant and control stimuli (collapsed in the analysis because these stimuli only started to differ after 100 msec) elicited a significantly larger N1 in the regular than the irregular condition [$F(1, 14) = 5.97, p < .05$; see Figure 5]. This result is compatible with the known refractory properties of the N1 wave (Näätänen & Picton, 1987). No other main effect or interaction reached the level of significance.

Discussion

Many of the previous studies of MMN have used a regular presentation procedure. We examined this procedure with a 7-sec interval between tones, along with an irregular presentation procedure in which the standard tones were much closer together but the interval between the last standard and the deviant tone still was 7 sec. The finding was clear. Even though no MMN was elicited in some of the participants in the irregular

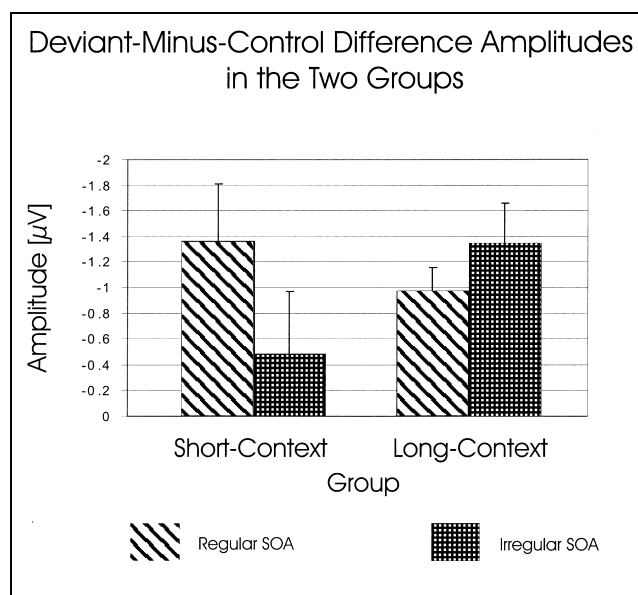


Figure 6. Experiment 2. Fz group-average deviant-minus-control difference-wave amplitudes in the regular (slanted-line pattern) and irregular (square pattern) conditions for the short-context and the long-context groups. (See the measuring algorithm in Methods and the measurement intervals in Table 3.) Standard errors of mean (S.E.M.) are displayed on top of each bar.

Table 3. Experiment 2. Fz Deviant-Minus-Control Peak, 50% Peak Amplitude (Measurement Start and End) Latencies (in ms From the Stimulus Onset), and Average Deviant-Minus-Control Difference Amplitudes (in $\mu\text{V} \pm \text{S.E.M.}$) of Possible MMN Responses in the Short Context and Long Context Groups (See Results) in the Regular and Irregular Conditions

Condition	Short context group				Long context group			
	Start	Peak	End	Amplitude	Start	Peak	End	Amplitude
Regular	204	240	264	-1.36 ± 0.45^a	244	292	376	-0.97 ± 0.20^b
Irregular	268	280	304	-0.48 ± 0.45	220	296	384	-1.34 ± 0.32^b

The marked significance levels were obtained by one-sided dependent *t* tests between the deviant and control response amplitudes in the given groups/measurement ranges.

df=6 (short context group) and 8 (long context group).

^a*p* < .05.

^b*p* < .01.

condition (the basis for referring to them as the short-context group), those same participants did show an MMN in the regular condition. So did the remaining (long-context group) participants, who in fact showed an MMN in both conditions. This result is compatible with those of Czigler et al. (1992) who found a clear MMN in their 7.2-sec SOA regular stimulus presentation paradigm. In the present experiment, the overall superiority

of the regular condition for producing MMNs occurred even though the nonfinal standards (the ones preceding the last standard of the train) were temporally much closer to the deviant in the irregular condition than they were in the regular condition.

These results cannot be interpreted on the basis of the cumulative strength of the sensory memory trace of the standard tone, which, at the time when the deviant arrives, should be at least as strong in the irregular condition, inasmuch as that condition allowed less time for the decay of sensory memory for the nonfinal standard tones. The results can be explained instead with appeal to the large-scale memory organization of the acoustic stream (Cowan et al., 1997; Bregman, 1990). The notion would be that the representation of the standard tone can become ineffective after a silent period not only if it has faded from a sensory memory store, but also if it has not faded but nevertheless is no longer regarded as currently relevant by the preattentive auditory mismatch detection system. The relevance presumably would depend on (1) the ratio of the interstandard interval (the time between successive standards) to the predeviant interval (the time between the last standard and the deviant) and on (2) the absolute duration of the predeviant interval. The present results demonstrated that, at a 7-sec predeviant interval, a <1.0 ratio of the interstandard to the predeviant interval prevented the elicitation of the MMN in some subjects in whom MMN was elicited at the regular (1.0 ratio) presentation rate. In contrast, at a 4-sec predeviant interval, Grau et al. (1998) found no difference between the MMN elicited in their regular condition and the comparable irregular condition including a 0.3-sec interstandard interval, where the interstandard to predeviant interval ratio was close to the present one. Thus, it seems that the interstandard to predeviant interval ratio alone cannot account for the presence or absence of the MMN. Two other factors that appear to play a role are the absolute duration of the interstandard interval (e.g., Sams et al., 1993; Mäntysalo & Näätänen, 1987) and, given the present results in contrast to those of Grau et al.'s, the absolute duration of the predeviant interval.

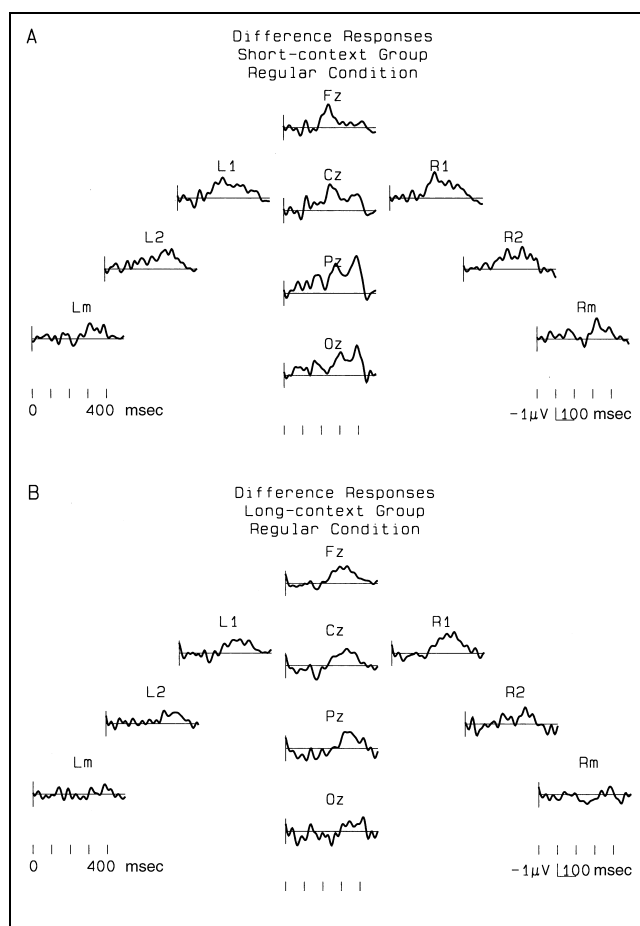


Figure 7. Experiment 2. Deviant-minus-control difference curves from all recording locations in the regular condition for the short-context (A) and long-context groups (B).

It is likely that the long-context group processed the tones similarly, but with a longer period before the standard tone group became irrelevant for the mismatch detection process. One indication of this similarity between subgroups is that, in Experiment 1, no MMN was obtained from any of the experimental participants in the irregular presentation procedure with a 10-sec predeviant interval, just as Cowan et al. (1993) obtained no MMN for a deviant immediately following an 11- to 15-sec predeviant interval with irregular stimulus presentation. Another indication is that the only previous study using a regular presentation procedure with a longer than 10 sec intertone interval (Sams et al., 1993) still obtained an MMN in about half of the subjects, whereas the present Experiment 2 as well as Czigler et al. (1992) recorded an MMN in all subjects in a regular 7-sec SOA condition.

GENERAL DISCUSSION

In Experiment 1, only some participants produced an MMN to a duration deviant in an irregular condition in which tones were presented with a short, 0.5-sec SOA between standards and with a much longer, 7-sec SOA between the last standard and the duration deviant. In Experiment 2, participants who did not produce an MMN in that situation nevertheless did so in a regular condition in which a 7-sec SOA was used between all tones. These results demonstrated that the temporal schedule of stimulus presentation can affect the elicitation of the MMN response not only via the decay of the standard-stimulus sensory memory trace but also by the large-scale organization of the auditory stimulus sequence in memory. Therefore, although the presence of the auditory sensory memory trace of the repetitive standard sound may be a necessary precondition of MMN elicitation when occasional deviant sounds differ from this standard sound, it is not a sufficient precondition even in such situations (see also Winkler, 1996). The present results support the notion that the memory directly involved in the MMN-generating process contains records of the detected regularities of the auditory stimulus sequence rather than only a sensory memory trace of the repetitive standard stimulus (cf. Ritter et al., 1998; Schröger, 1997; Winkler, Karmos, et al., 1996; Cowan et al., 1993).

An account of the present results can be based on the notion of contextual relevance. One may assume that MMN is only elicited if the deviant stimulus is grouped together with the preceding regular stimuli; that is, that each regularity is relevant only within its own memory group. In the regular condition of Experiment 2, unlike in the irregular conditions of both experiments, there were no temporal cues that would signal the end of one tone group and the beginning of another, so the repetitive standard presumably remained relevant to the mismatch process. In accordance with this account, Cowan et al. (1993) suggested that it may be the

diminished contextual relevance of the standard as time passes that is critical for the MMN, rather than the diminished vividness of the sensory memory trace. Winkler, Karmos, et al. (1996) further developed this point, proposing a “model adjustment hypothesis” to explain MMN phenomena. According to this hypothesis, MMN is generated on the basis of a model of the auditory environment. This model stores records of preattentively detected regularities of the recently heard sounds. Incoming stimuli are compared with sensory inferences based on the detected regularities. When these implicit expectations are violated, the model is updated, accommodating it to the change in the acoustic environment. The MMN component is involved in adjusting the model (see also Winkler & Czigler, 1998). The model adjustment hypothesis could account for the present results with the claim that, following a train of identical tones, a sufficiently long silent interval eliminates any implicit expectation for the nature of the stimuli that may follow and, therefore, precludes the possibility of an MMN to the deviant being obtained.

Explaining the present results in terms of contextual relevance receives strong support from studies showing that perceptual grouping (such as the ratio rule) affects performance in memory recall tasks (see, e.g. Nairne, Neath, Serra, & Byun, 1997). The paradigm most comparable to the present one is the two-tone comparison procedure of Cowan et al. (1997) in which both the time between trials and the time between tones within a trial were manipulated. In particular, when the intertone interval was 6 sec, close to the 7 sec between the last standard and the deviant stimulus in the present irregular condition, tone-comparison performance was higher at a 12-sec than at a 3-sec intertrial interval. At the latter intertrial interval, the ratio of intertrial to intratrial (intertone) interval was 1:2. In the present study, the intertrial interval was actually under 0.5 sec (the duration from the start of the deviant/control tone of one trial to the start of the first standard of the next trial), producing a ratio of 0.5:7 or 1:14. Cowan et al. (1997) did not test ratios that unfavorable but their least favorable ratio, 1:4, led to a performance level that was even lower than that obtained at the 1:2 intertrial to intratrial interval ratio. Thus, it is quite possible that the preperceptual memory organization that was assumed on the basis of the present MMN results is closely related to the perceptual organization of memory that can be observed in behavioral studies.

It is, however, possible that grouping in the present study was not entirely preperceptual. Reading a book possibly allows subjects to covertly attend the auditory stimuli even if they had no task related to them. Thus, subjects could have grouped the tone sequences attentively. However, the ERP results recorded in the present experiments did not show the typical signs of attention, (i.e., attended deviant sounds elicit an N2b and a P3 component; for a review, see Näätänen, 1992). The

tendency for polarity reversal at the mastoid leads, characterizing the MMN but not N2b, was present in the traces of all deviance-related negativities (see Figures 4 and 7) while no positive wave followed these MMN responses (except for the 0.5-sec predeviant interval in Experiment 1; see Figures 2 and 5). Since the elicitation of the MMN component does not require that the subject should focus his/her attention on the auditory stimuli, the present results seem to reflect the effects of preattentive large-scale grouping of the auditory stimulus sequence.

The time course of the loss of relevance of the standard sequence for the MMN process (as suggested by the present results) appears to agree well with phenomena in the recent behavioral literature. One compelling behavioral example is the finding that a repeating tone sequence biases a later alternating sequence toward segregation into two streams in a manner that falls off precipitously as the time between the repeating and alternating sequences increases to about 8 sec (Beauvois & Meddis, 1997), demonstrating that the time course of the longer auditory sensory memory discussed by Cowan (1984, 1995) may well be relevant to perceptual grouping phenomena. This time course is similar to the present finding that, in the irregular presentation condition, some participants ceased to show an MMN with a 7-sec predeviant interval and all ceased to show an MMN with a 10-sec interval (in Experiment 1).

The present finding makes an intriguing contribution to models of information processing. The vast majority of previous studies regarding the perceptual grouping of stimuli over a large time scale (e.g., Bregman, 1990) depended upon behavioral methods in which participants had to listen to the stimuli and make voluntary responses. Thus, it remained unclear whether the grouping depended on deliberate attention to the stimuli or not. Since the MMN is elicited even when the participant's attention is directed to other, irrelevant visual or auditory stimuli (e.g., Alho & Sinervo, 1997; Winkler, Cowan, Csépe, Czigler, & Näätänen, 1996; Paavilainen, Tiitinen, Alho, & Näätänen, 1993; Schröger, Näätänen, & Paavilainen, 1992), the implication is that large-scale auditory grouping can occur in memory preperceptually without willful attention. This conclusion receives further support from Sussman et al.'s (1999) results demonstrating that auditory streaming can also occur without deliberate attention (see Introduction). Although the notion of preattentive grouping is not common in theories of auditory stimulus processing (Darwin, 1997), preattentive popout of object clusters grouped on the basis of a common feature have been observed in several studies of visual perception (e.g., Nothdurft, 1990; Julesz, 1981). For example, if a printed character array contains a cluster of instances of the letter "L" surrounded by instances of the letter "O", the group of "L" letters will form a larger-scale object

that preattentively appears to "pop out" from its background.

When examining models of auditory processing in detail, it becomes evident that there are several, slightly different ways to interpret the present findings, which will have to be differentiated in future research. One way is to assume that both absolute and relative amounts of time are important in processing, an assumption made in at least two recent behavioral studies (Cowan et al., 1997; Nairne et al., 1997). There are different possibilities for what it is that depends on absolute time and what it is that depends on relative time. It may be that the last standard tone and the deviant both must fall within some limited time period (e.g., perhaps 10 sec), whereas the contextual relevance of the standard also is necessary and depends on relative timing, or on both absolute and relative timing (see the Discussion of Experiment 2). Another view would also acknowledge the importance of the relative timing of standards and the deviant, but would further emphasize that the absolute amount of time could be important not only for a simple sensory memory trace, but also for the memory of the higher-order features of an auditory perceptual object, which decay over time perhaps with a different rate than that of the simple auditory stimulus features. Finally, an even more radical view is that only relative amounts of time are relevant. On one hand, arguments have been offered against this view, including the finding by Grau et al. (1998) that at a short (4-sec) predeviant SOA, the relative timing of the standard and deviant stimuli did not seem to affect the elicitation of the MMN, and the finding by Sams et al. (1993) that a regular presentation with a 10-sec SOA did not produce an MMN consistently. On the other hand, within these studies another relative timing factor, the proportion of time taken up by the tone stimuli, was not considered. In order to test one version of this "temporal relativity" view, it would be necessary to allow the duration of tones to covary with the SOA so that they would make up a constant proportion of the full presentation time of the auditory sequence regardless of the SOA. Although the present article cannot address such nuances, it does clearly establish that the MMN depends at least partly upon contextual factors of tone grouping that are very different from decaying auditory sensory memory.

METHODS

Experiment 1

Experimental Participants, Procedure, and Stimuli

Altogether, 15 healthy experimental participants (seven female, 17–37 years of age) were tested, eight in Budapest (Institute for Psychology, Hungarian Academy of Sciences), seven in Munich (Department of Psychology, Ludwig Maximilians University) using identical equipment and procedure.

During the EEG recordings, the experimental participant was instructed to read a book of his/her choice and to disregard the auditory stimuli. The experiment consisted of two identical sessions that were run on separate days.

Sixteen blocks of 588 simple tones (600 Hz, 80 dB, 5–5 msec rise and fall times) were binaurally presented via headphones to experimental participants (9,408 tones altogether by the NeuroStim stimulation system). Each block consisted of 84 trains of seven tones. The first six tones were identical, having either 100-, 170-, or 300-msec stimulus duration (standards), the seventh tone was always 100 ms long (deviant/control stimulus). Each type of train appeared 28 times in a stimulus block. The stimulus onset asynchrony (SOA, onset-to-onset interval) preceding the standard tones (including the first tone of the trains) was always 0.5 sec. The deviant/control tone was preceded by a SOA of 0.5, 2, 7, or 10 sec. The four different predeviant intervals appeared equiprobably within each type of stimulus train. The order of the 12 different stimulus sequences (3 different standards \times 4 predeviant intervals) was randomized separately for each block. Each stimulus sequence received 112 repetitions during the experiment (16 blocks \times 7 sequences/block).

EEG Recording, Data Processing, and Statistical Testing

EEG was recorded (NeuroScan EEG system) with a digitizing rate of 250 Hz by Ag/AgCl electrodes from 10 scalp locations: Fz, Cz, Pz, and Oz, the two mastoids, and at 2–2 locations over each hemisphere (L1, L2 and R1, R2) placed at the one and two-thirds division points of the arc connecting Fz to the mastoid. The common reference electrode was attached to the tip of the nose. The horizontal electrooculogram (HEOG) was recorded bipolarly from electrodes placed near the outer canthi of both eyes. The vertical EOG was recorded between electrodes attached above and below the right eye.

All EEG and EOG channels were filtered between 1 and 30 Hz (24 dB/octave). ERP responses were represented by epochs of 550-msec duration starting at the stimulus onset. After rejecting epochs with an EEG or EOG change exceeding 100 μ V the responses were averaged separately for each type of sequence and the position of the stimulus within the sequence. Slow shifts that remained in the data due to the relatively small number of repetitions in some stimulus classes were reduced by linear detrending.

Amplitude measurements were referred to the average amplitude of the first 50 msec of the epoch (because each tone was identical within the first 100 msec from the stimulus onset). N1 measurements were taken at Cz, MMN measurements at Fz, based on the well-known scalp distributions of these ERP components. MMN responses were measured from the difference between the response to a given type of deviant and that to the

corresponding control stimulus (the same, 100 msec long, stimulus following a sequence consisting of 100-msec duration standard stimuli and preceded by the same SOA as the corresponding deviant). Amplitude and area measures were calculated from intervals around the peak of each grand/group-average difference. Peak latencies were determined from each deviant-minus-control difference response by finding the most prominent negative (or negative going) peak in the 200- to 300-msec poststimulus interval (as MMN was expected to peak between 100 and 200 msec from the onset of deviation that, in the present experiment, was at the offset of the deviant stimulus, at 100 msec from the stimulus onset). The start (and end) of the measurement intervals were set at the latencies where the difference amplitude first (and last) exceeded 50% of the peak amplitude. In addition, peak latencies were measured separately for each individual experimental participant.

The elicitation of the MMN response was verified by one-sided dependent *t* tests. Comparisons between conditions and groups were conducted by mixed analyses of variance of dependent (conditions) and independent (groups) variables (Huynh–Feldt corrections included where applicable) and by dependent and independent *t* tests. All significant results are discussed.

Experiment 2

Twenty healthy experimental participants (10 female, 22–38 years of age) were tested, all of them in Munich (Department of Psychology, Ludwig Maximilians University).

During the EEG recordings, the experimental participant was instructed to read a book of his/her choice and to disregard the auditory stimuli. The experiment consisted of one session.

Twelve blocks of 160 simple tones (600 Hz, 80 dB, 5–5 msec rise and fall times), each were binaurally presented via headphones to experimental participants (1,920 tones altogether by the NeuroStim stimulation system). Blocks consisted of 40 stimulus trains of four tones, each. The first three tones were identical (standards) with 100-msec stimulus duration in one half and 300-msec stimulus duration in the other half of the blocks. The fourth stimulus following 7-sec SOA was either identical to the first three tones (control stimulus), or (deviant) had the opposite stimulus duration (300 msec after the 100 msec long standards, 100 msec after the 300-msec standards). Control and deviant trains were presented equiprobably in each block. In half of the trains, the standard stimuli were preceded by a 7-sec SOA (the regular condition), in the other half, standards were preceded by 0.5 sec SOA (the irregular condition). The four different types of sequences (2 conditions \times 2 types of train ending) were randomized separately for each stimulus block. The order of the stimulus blocks

with 100-msec and 300-msec standard tones was balanced. Altogether, each type of sequence received 60 repetitions (6 blocks/standard × 10 sequences/block).

EEG recording, data processing, and statistical testing was similar to Experiment 1. MMN responses were assessed from subtractions between deviant and control responses of identical stimuli. The control for a given deviant was taken from the blocks with reversed standard/deviant durations (e.g., the response to a 300-msec deviant [100-msec standard blocks] in the irregular condition was compared with the response to the 300-msec control stimulus [300-msec standard blocks] of the same condition). The MMN responses elicited by the two different deviants (corresponding conditions in the blocks with reversed standard/deviant durations) were collapsed to achieve sufficient numbers of repetitions (120) for deviant and control stimuli in each condition. The deviant-minus-control difference-wave peaks were determined from the 200- to 300-msec poststimulus interval for all cases (similarly to Experiment 1). However, due to the long duration of some of the MMN components obtained in this experiment, measurement intervals could extend beyond 300 msec (i.e., the latency of the 50% peak-amplitude point following the peak could fall into the 300–400 msec range).

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