Temporal integration of auditory stimulus deviance as reflected by the mismatch negativity

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Abstract

We recorded event-related brain potentials (ERPs) to two different infrequent deviant tones presented successively within the repetitive sequence of a standard tone. A separate mismatch negativity (MMN) component was elicited by each of the two deviants when the interval separating their onsets was 300 ms. However, only a single MMN component was elicited when the temporal separation between the onsets of the two deviants was 150 ms. Previous studies obtained similar results using two temporally separated deviations carried by a single sound. Taken together, these results support the notion of a general temporal integration mechanism in the formation of auditory events with ca. 200 ms long window.

Keywords: Audition; Temporal integration; Event-related potentials; Mismatch negativity; Auditory event formation

Auditory object formation appears to be susceptible to the time course of events in the early phases of auditory processing. Detection of a given stimulus event can be influenced by the proximity of the surrounding stimulus events. Temporal factors that affect auditory event formation have recently been studied using event-related brain potentials (ERPs) [12,14]). The mismatch negativity (MMN [6], for a recent review, see Ref. [11]) ERP component is especially useful in such investigations as it reflects pre-attentive detection of infrequent changes in a regular flow of auditory stimulation. The elicitation of MMN signals the detection of an auditory event (the stimulus change). It provides information about the encoding of the deviant event and also about the encoding of the previous stimulus events which form the basis for change detection. The typical way to elicit the MMN is to present rare auditory stimuli (deviants) within a repetitive sequence of a frequent sound (standard).

In this case, the deviant sound elicits a negative wave, the MMN, which is maximal over fronto-central scalp locations and often inverts in polarity below the Sylvian fissure. This topography suggests that the main generators of this component are located in the auditory cortex [1]. The MMN typically peaks between 100 and 200 ms from the onset of stimulus deviance. MMN is elicited even when the subject is absorbed in a task that is not related to detecting the deviant stimuli or to the auditory stimulation in general [2]. Therefore, MMN provides a way to study the contents of transient auditory memory (what constitutes the ‘standard’) and the automatic formation of auditory events.

Czigler and Winkler [3] studied the question of auditory event formation by presenting deviant sounds that differed from the repetitive standard sound along two stimulus dimensions (frequency and duration). Deviation in frequency commenced at the onset of the deviant stimulus, whereas deviation in stimulus duration could only be detected after the offset of the 100-ms long deviant stimulus (270-ms standard duration). Because the feature deviations were temporally offset by 100 ms, detection of them could only occur in a serial manner. Since only one MMN was obtained the authors suggested that the two temporally separate deviations carried by the same stimulus were processed as a single deviant event.
In a follow-up study Winkler et al. [14] used two different temporal separations: deviants differed from the standard in their intensity and in the direction of the frequency glide segment commencing at 150 or 250 ms from the onset of the tones. They replicated Czigler and Winkler’s [3] findings that only one MMN is elicited when the two deviations occur within 150 ms of each other. However, when these deviations were separated by 250 ms, two MMNs were obtained. This suggests that the auditory system integrates successive deviations, appearing on the same stimulus, to unitary deviant events when they fall within ca. 200 ms period.

The above studies employed successive violations of the same auditory regularity: both features of the rare stimulus deviated from the same repetitive standard stimulus. Winkler and Czigler [13] hypothesized that violations of two different regularities might constitute separate deviant events, even if the two deviations fall within the 200 ms temporal integration period. Therefore, they presented rare stimuli that deviated from two different regularities. Rare tones broke the pattern of frequency alternation of the auditory sequence (by repeating the frequency of the previous tone [7], and were shorter (150 ms) than the alternating standard tones (270 ms). Their result, two temporally separated MMNs within 150 ms elicited by the two deviations of the single double-deviant tone, indicates that integrating the deviant elements of a single sound cannot be explained by temporal proximity alone.

Taken together, the above results indicate that two temporally separate deviations are processed as a single deviant event if they occur on a single stimulus within ca. 200 ms and both violate the repetition of the same stimulus. However, the temporal integration process [5,16] is probably not restricted to integration within a single sound. Plomp’s results [9] showing that a noise burst can be perceived as the continuation of the preceding noise burst (even though separated by a short gap) suggest that the auditory system integrates discrete stimulus elements across time. On this basis, one may expect that integration of two successive deviances could also occur if these deviances are carried by two discrete auditory stimuli. However, it is also possible that integration between temporally separate deviations occurs only within a single stimulus, perhaps as part of the feature integration process that results in the unitary perception of discrete auditory stimuli. Therefore, the purpose of the present experiment was to determine whether or not the characteristics of the integration process observed for single deviant stimuli also apply to successive deviations carried by discrete auditory stimuli.

In the present study, two kinds of deviant stimuli occurred within an unattended sequence of a repetitive standard stimulus with the constraint that there were always two deviant stimuli presented in a row: every time a frequency-deviant stimulus occurred it was followed by an intensity-deviant stimulus. Two different rates of stimulus presentation were chosen, one in which the two successive deviants fell within 200 ms and one in which the two deviants were separated by more than 200 ms. A third condition was introduced to test whether or not it is possible to elicit two MMNs by two successive separate deviant stimuli within 200 ms, based on Winkler and Czigler [13] that demonstrated the elicitation of two temporally separated MMNs within 150 ms for deviations appearing on the same stimulus.

If the process integrating successive deviations were specific to deviations occurring within a single stimulus, the elicitation of two successive MMNs should be expected in all three conditions, because two successive separate deviant stimuli were presented in all three conditions. If, on the other hand, the process integrating successive deviations were a general characteristic of early auditory processing (i.e. not limited by the borders between separate stimuli), only a single MMN should be elicited when the frequency deviant is immediately followed by the intensity deviant within 200 ms. If auditory deviations in discrete stimuli are processed similarly to the way it was found for continuous sounds, the elicitation of two separate MMNs can be expected when the two successive deviants are separated by more than 200 ms [14], or when the two deviants violate two different regularities of the preceding auditory sequence [13].

Twelve paid, healthy adults (one male) ranging in age from 25–41 years participated in the experiment. The data from three of the participants were excluded due to excessive artifact. Participants read books during the session and were instructed to ignore the tonal stimuli. Eye movements were monitored on-line to ensure that the participants read during the testing session. The testing procedure was explained to all participants before informed consent was obtained.

Stimuli were 50 ms pure tones delivered binaurally through insert earphones, in three conditions: FI-150, FI-300 and AI-150 ms. In the FI-150 and FI-300 ms conditions, standard tones, occurring on 85% of the trials, had a frequency of 440 Hz and an intensity of 75 dB SPL. Frequency deviant tones (494 Hz–75 dB) occurred randomly on 7.5% of the trials always followed by the intensity deviant tone (440 Hz–65 dB). The difference between the FI-150 and FI-300 ms conditions was the stimulus onset asynchrony (SOA; 150 and 300 ms, respectively). In the AI-150 ms condition, the standard sequence was an alternating pattern of two tones of 440 and 494 Hz frequencies, 75 dB in intensity, presented at a 150 ms SOA. The alternation deviant (a break in the alternating pattern by repeating the 494 Hz tone) occurring on 7.5% of the trials was always followed by an intensity deviant (65 dB–440 Hz). Two blocks of 1500 stimuli (225 deviants of each type) were collected for each condition. The order of the conditions was counter-balanced across participants.

Electrical brain activity was recorded using direct-coupled amplifiers with a low-pass filter setting of 40 Hz and a digitization rate of 250 Hz. The epoch duration was...
800 ms, which included a 100 ms pre-stimulus baseline. Recordings were done using a 32-channel electrode cap which included the following electrode sites: Fpz, Fz, Cz, Pz, Oz, Fp1, Fp2, F3, F4, F7, F8, FC5, FC6, FC1, FC2, T3, T4, C3, C4, CP5, CP6, CP1, CP2, T5, T6, P3, P4, O1, O2 of the 10–20 system and LM, and RM (left and right mastoids, respectively). The common reference electrode was placed on the tip of the nose. Voltage changes in the electro-oculogram (EOG), caused by horizontal eye movements were monitored at electrodes F7 and F8, and those caused by vertical eye movements and blinks, were monitored in a bipolar electrode configuration using FP1 and an electrode placed below the left eye. Artifact rejection was set to omit activity exceeding ±100 μV at any channel. EEG was digitally filtered off-line (bandpass 1–30 Hz).

ERPs were averaged separately for each stimulus type and condition. Difference waves were calculated by subtracting the ERP elicited by the standard of a given condition from those elicited by the deviant stimuli in that condition. MMN amplitudes were measured for each subject using a 50 ms window centered on the grand-average MMN peak which was determined separately for each condition at Fz. Amplitude measurements were referred to the mean voltage of the 100-ms pre-stimulus interval. To verify the presence of the MMN response for a given condition/deviant, the ERPs elicited by the standard and deviant stimuli were statistically compared using a two-way repeated measures analysis of variance (ANOVA) with factors of stimulus type (standard and deviant) and electrode (Fz, Cz, FC1, FC2, LM and RM). The Greenhouse–Geisser correction was applied when appropriate. The alpha level criterion was set at $P < 0.05$.

Fig. 1 shows the responses to the standard and deviant stimuli, together with their respective differences for the three experimental conditions. When the SOA between the two deviants in a row (frequency followed by intensity) was 300 ms (FI-300 ms condition), two successive MMNs were elicited ($F = 37.91$, df = 1,8, $P < 0.001$ and $F = 45.28$, df = 1,8, $P < 0.001$, respectively). In the grand-average difference curves, the first MMN peaked at 172 ms from the onset of the frequency deviant, the second at 161 ms from the onset of the intensity deviant. This result is compatible with those from other MMN studies in which two different feature deviants occurred successively in a row at long (>300 ms) SOAs [8]. However, when the SOA between consecutive stimuli was 150 ms, only a single, prominent MMN ($F = 40.07$, df = 1,8, $P < 0.001$) was obtained for the two successive (frequency and intensity) deviants (FI-150 ms condition). This MMN peaked at 156 ms from the onset of the frequency-deviant stimulus. The latency of this MMN indicates that it was elicited by the first of the two deviants in a row (the frequency deviant), whereas no negative deviant-minus-standard difference can be seen between 100 and 200 ms from the onset of the intensity deviant immediately following the frequency deviant.

In the FI-150 ms condition, a small, but statistically significant ($F = 6.093$, df = 8, $P < 0.05$), negativity (followed by a small positivity) can be seen in the difference waves at about 450 ms from the onset of the first (frequency) deviant (Fig. 1). This negative difference is far too late to be an MMN elicited by the second (intensity) deviant. It peaks 300 ms after the onset of this deviant, which is 150 ms after the onset of the first standard tone following the two consecutive deviants. Judging from its timing, this negativity is probably an MMN elicited by the standard stimulus immediately following the two deviant stimuli. MMN has been obtained to standard stimuli even when they followed a single deviant tone [8,10,15].

It is possible that only one MMN was obtained in the FI-150 ms condition because the MMN generators were in a state of refractoriness due to the rapid rate of stimulation. However, it has previously been demonstrated that MMNs elicited by deviance in different stimulus features are generated by at least partially separate neuronal generators [4]. Since the two deviants of the FI-150 ms condition deviated from the standard tone in different stimulus features, at least part of their neuronal generators should be separate and thus some MMN should have been elicited by the second deviant in the row. The results of the AI-150 ms condition also argue against the refractoriness explanation. Two significant MMNs were obtained in this condition ($F = 6.69$, df = 1,8, $P < 0.05$; $F = 20.77$, df = 1,8, $P < 0.01$, respectively), when the deviations occurred on successive stimuli only 150 ms apart. The first MMN peaked at 172 ms from the onset of the alternative deviant, the second at about 200 ms from the onset of the intensity deviant. Since the deviant stimuli and the SOA were identical between the FI-150 ms and the AI-150 ms conditions, it is very unlikely that refractoriness could have so drastically affected the MMN elicitation in one condition but not the other. The results of the AI-
150 ms condition are compatible with Winkler and Czigler [13] showing two separated MMNs when the two deviations of their double-deviant stimuli, which violated different types of regularities, occurred within 200 ms of each other.

The present MMN results suggest that integration of two deviant stimuli in a row to a single deviant event only occurs when the two deviants are presented within a 200 ms interval, which is compatible with the results obtained in studies using temporally separated double deviants on single stimuli.

For the conditions within which the deviations were separated by a 150 ms interval, one MMN was elicited when the two deviations (frequency and intensity) violated the repetition of a single standard stimulus, whereas two MMNs were obtained when the two deviations violated different types of regularities of the preceding auditory sequence. This latter result cannot be explained by temporal promixity alone. Apparently, as was also demonstrated by Winkler et al. [13,15], the system underlying the MMN maintains separate representations of the different detected regularities. The integration of deviations within a 200-ms interval is limited to violations of the same detected regularity.

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