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Determinants of the auditory mismatch response

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Summary The auditory mismatch field (MMF) is supposed to reflect a comparison process between an infrequent deviant stimulus and the memory trace left by frequent standard stimuli. Therefore, the MMF amplitude has been thought to depend on the strength of such a trace. We examined this hypothesis in records with a 24-channel planar SQUID magnetometer by varying the number of stimuli preceding each deviant, the interdeviant interval (IDI) and the interstimulus interval (ISI) just preceding the deviant (pISI). When a constant IDI was employed and the number of standards between two deviants varied in different sessions, MMF amplitude increased as the number of standards increased. However, MMF did not depend on the number of standards between two deviants when the number varied within a single session and ISI varied as well. MMF decreased slightly when pISI increased from 0.6 to 3.4 sec. When IDI increased and the ISI remained constant, MMF amplitude increased. Most results can be explained within the framework of the memory-trace hypothesis of MMF generation. However, the strengthening of the trace seems to be a complex process which is also affected by the temporal features of the stimulus sequence.

Key words: Magnetoencephalography; Mismatch field; Oddball paradigm; Auditory cortex; Memory trace; Current dipole; (Human)

In oddball-paradigm experiments, in which frequent ("standard") and infrequent ("deviant") stimuli are presented in random order, mismatch responses (MMRs) are observed in both attend and ignore conditions. The MMR is called the mismatch negativity (MMN) and mismatch field (MMF) in electrical and magnetic records, respectively. According to Näätänen (1984, 1992), the MMN is related to a comparison process between the deviant input and the memory trace produced by the standard stimulus.

The amplitude of MMN depends on the relative probabilities of the standards and deviants; the lower the probability of the deviants, the larger the MMN (Näätänen et al. 1983). When the stimulus sequence consists of two equiprobable tones, each elicits an MMN when preceded by a few dissimilar stimuli, demonstrating that the MMN amplitude is determined by the local probability of the stimuli (Sams et al. 1983). These results suggest that repetition of the standard stimulus strengthens the corresponding memory trace.

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The duration of the memory trace has recently been studied by varying the interstimulus interval. The assumption is that the longer the interval between the standard and the deviant the weaker the memory trace for standards when a deviant occurs and, hence, the smaller is the MMR. Mäntysalo and Näätänen (1987) found a statistically significant MMN at short ISIs up to 2 sec but not at 4 and 8 sec ISIs. However, MMN has been obtained recently at ISIs of 7.2 sec (Czigler et al. 1992) and even 10 sec (Böttcher-Gandor and Ullsperger 1992). A significant MMF was obtained at 9 sec but not at 12 sec ISI (Sams et al. 1993); in this study, behavioral and neuromagnetic measurements gave rather similar estimates for the trace duration.

However, the effect of the ISI on the amplitude of the mismatch response is unexpectedly small (Näätänen et al. 1987; Böttcher-Gandor and Ullsperger 1992; Czigler et al. 1992; Sams et al. 1993). A crucial factor here might be the interplay between ISI and temporal probability of the deviants. When the ISI is made shorter, keeping the sequential probability of the deviants constant, the latter occur with shorter interdeviant intervals (IDIs). When the deviants occur in close succession, the corresponding mismatch processes may weaken (Näätänen et al. 1987). Actually, when two deviants follow each other, the latter elicits a much smaller MMN than the former (Sams et al. 1984).

The memory trace hypothesis, supported by experimental data, suggests that (i) the trace is reinforced by stimulus repetition, (ii) it has a decay time of about 10 sec, and (iii) the frequently occurring deviants elicit weak mismatch responses. The following 3 experimental hypotheses were formulated to verify and further investigate the memory trace interpretation of the MMR.

Hypothesis 1: MMF is affected by the number of standard stimuli between consecutive deviants within the memory trace duration: the larger the number of standards, the stronger the trace and the larger the MMF.

Hypothesis 2: MMF is affected by the immediately preceding interstimulus interval (pISI) because the memory trace for the standard stimulus decays over time. The longer the interval between the last standard stimulus and the deviant stimulus, the weaker the standard memory trace, and thus the smaller the MMF.

Hypothesis 3: MMF is influenced by IDI: the longer the IDI, the stronger is the neural activity caused by the deviant, and the larger the MMF.

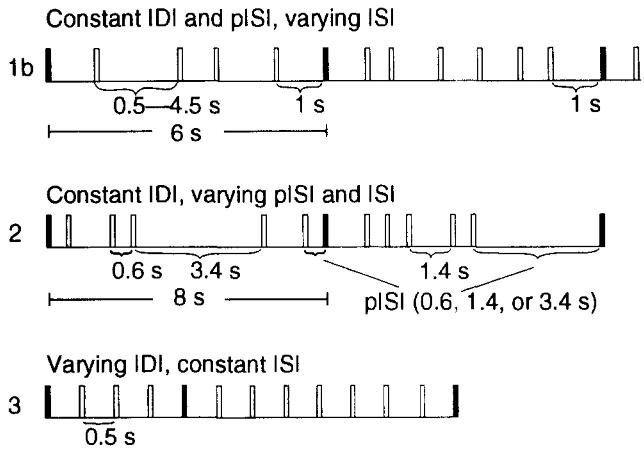

Fig. 1. Schematic illustration of stimulus sequences in experiments 1b, 2 and 3. Filled symbols indicate deviants and open symbols standards. In experiment 1b, IDI was always 6 sec and pISI was always 1 sec. The number of standards between deviants varied from 2 to 8. ISI varied randomly (within the constraints imposed by the constant IDI, the constant pISI and the number of standards) between 0.5 and 4.5 sec. In experiment 2, IDI was constantly 8 sec and there were always 5 standards between deviants. Three ISIs were used: 0.6, 1.4 and 3.4 sec. There were always three 0.6 sec ISIs, two 1.4 sec ISIs and one 3.4 sec ISI between two deviants. Deviants were averaged into 3 classes depending on the pISI. In experiment 3, IDI varied between 2 and 8 sec. ISI was constantly 0.5 sec and thus the number of standards between deviants increased as a function of increasing IDI.

Methods

Subjects and stimuli

Four experiments were designed to test hypotheses 1–3. Thirteen subjects in total were studied (9 members of the laboratory staff and 4 paid volunteers; 23–47 years; 7 males). The number of subjects participating in experiments 1a, 1b, 2, and 3 was 6, 7, 7 and 6, respectively. During recording, the subject lay on a wooden bed in a magnetically shielded room with his or her head fixed in a vacuum-cast pillow and read a self-selected book.

The stimuli were transformed into acoustic form by a TDH-39 earphone located outside the magnetically shielded room and were delivered to the subject's left ear through a plastic tube. Details of the stimuli are given below.

Experiment 1a was designed to test hypothesis 1. We changed the number of standards between deviants and kept IDI constant (10 sec). Thus there were corresponding changes in stimulus probability and in ISI. Stimuli were 30 msec sinusoidal tones, with 5 msec rise and fall times. Standards were 1 kHz and deviants 1.2 kHz in frequency. The number of standards between two deviants was 3, 9 or 19 in different sessions. The sequential probability of the deviant was thus 0.25, 0.1 or 0.05, and the ISI 2.5, 1 or 0.5 sec, respectively.

Experiment 1b further tested hypothesis 1, but now we also kept the long-term deviant probability constant by presenting all different sequences within the same stimulus train. Stimuli were 20 msec sinusoidal tones, with rectangular envelopes. Standards were 1 kHz and deviants 1.1 kHz in frequency. The number of standards between two deviants was 2, 4, 6 or 8, presented randomly within the same session. The IDI was always 6 sec and the pISI 1 sec but the other ISIs were allowed to change between 0.5 and 4.5 sec. The long-term presentation probability was 0.834 for standards and 0.166 for deviants (0.042 for each of the 4 classes of deviants). The deviants were classified into 4 groups depending on the number of immediately preceding standard stimuli. An example of the stimulus sequence is shown in Fig. 1.

Experiment 2 was designed to examine the dependence of MMF on pISI (hypothesis 2). In general it is impossible to change ISI without altering IDI or the deviant presentation probability (and thereby the number of preceding standards). We therefore used 3 different ISIs within the same session. We kept constant the IDI, the number of standards between deviants (and thus the deviant probability) and the long-term ISI, while varying pISI. Stimuli were 30 msec sinusoidal tones, with 5 msec rise and fall times. Standards were 1 kHz and deviants 1.2 kHz in frequency. IDI was 8 sec and the deviants were always separated by 5 standards. There were 3 possible ISIs (0.6, 1.4 and 3.4 sec). The order of the various ISIs was randomly chosen, but there were three 0.6 sec ISIs, two 1.4 sec ISIs and one 3.4 sec ISI between two deviants (cf., Fig. 1). Standards and deviants were each divided into 3 classes based on the pISI (0.6, 1.4, 3.4 sec). The probability of the standards was 0.444 for the 0.6 sec pISI, 0.278 for the 1.4 sec pISI, and 0.111 for the 3.4 sec pISI, yielding an overall probability of 0.833 for standards. Deviants had an overall probability of 0.167; each of the 3 classes had an equal probability of 0.056.

Experiment 3 examined the effect of IDI on MMF (hypothesis 3). The number of preceding standards changed as a function of IDI, but ISI and the long-term deviant probability were constant. Stimuli were 20 msec sinusoidal tones, with rectangular envelopes. Standards were 1 kHz and deviants 1.1 kHz in frequency. ISI was 0.5 sec and IDI was 2, 4, 6 or 8 sec. The different IDIs were presented randomly within the same session (cf., Fig. 1). Since ISI was constant and IDI varied, the number of standards preceding the deviant also varied. For the different IDIs, the number of standards preceding the deviant was 3, 7, 11 or 15. The presentation probability was 0.025 for each of the 4 deviants with a different IDI, and 0.9 for the standard.

Recording

The magnetic signals were measured over the right hemisphere contralateral to the ear of stimulation with a 24-channel SQUID gradiometer (Ahonen et al. 1991). This device uses a planar flux transformer configuration: its two orthogonal figure-of-eight loops per sensor unit measure the tangential derivatives $\partial B_z/\partial x$ and $\partial B_z/\partial y$ of B_z, the field component normal to the head, simultaneously at 12 locations 3 cm apart. The sensors cover a head area of 12.5 cm in diameter. The planar gradiometer detects the largest signal just above a current source, the location of which can often be determined with a single measurement without moving the instrument. The locations and orientations of the 24 sensors with respect to external landmarks of the skull were determined before each measurement by recording the magnetic field produced by 3 small coils fixed on the scalp at known locations (Knuutila et al. 1987).

The analog data were sampled at 500 Hz after bandpass filtering between 0.05 Hz and 100 Hz (high-pass slope 35 dB/decade, low pass slope greater than 80 dB/decade). The measurement time was 460–600 msec, including a pre-stimulus baseline of 60–100 msec in different experiments. The first two epochs of each experiment were omitted from the average.

The vertical electro-oculogram (EOG) was recorded to monitor artefacts from eye blinks and eye movements; responses coinciding with EOG deflections exceeding 150 μV were rejected from the average. The number of single responses averaged for each deviant was 67–100.

Analysis

Responses to different standards and deviants were selectively averaged. In exp. 1b, responses to the deviants were selectively averaged into 4 classes depending on the number of preceding standards. Responses to all standards, except those immediately after the deviant, were averaged together. In exp. 2, responses to standard and deviant stimuli were selectively averaged according to the different pISIs. MMFs were obtained by subtracting the response to the standard stimulus from the response to the deviant stimulus with the same pISI. In exp. 3, responses to the deviants

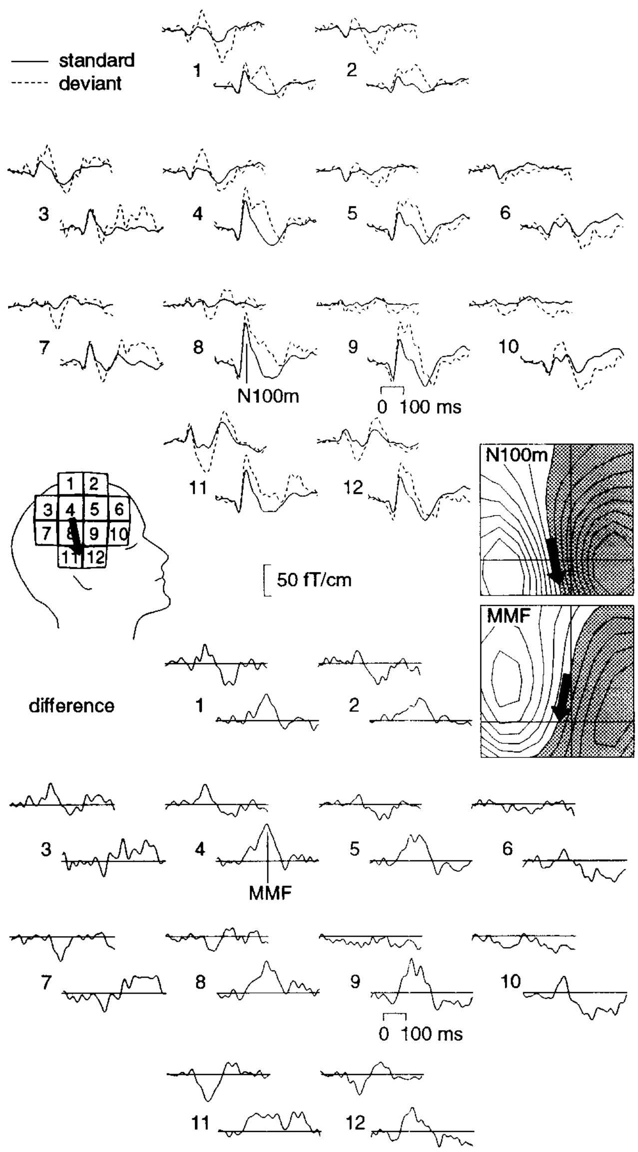

Fig. 2. Top: averaged magnetic responses of one subject to standard (solid lines) and deviant (dashed lines) stimuli when the number of intervening standards was 19. The N100m response is indicated. The 12 measurement locations are shown on the schematic head. At each location both the vertical ($\partial B_z/\partial y$) and the horizontal ($\partial B_z/\partial x$) gradients of B_z were measured. The upper curves of each response pair refer to the vertical and the lower curves to the horizontal gradient. Bottom: difference wave forms. The MMF is indicated. In the field patterns during N100m to standards and during the MMF on the right, the isocontours are separated by 20 fT/cm. The shadowed area indicates magnetic flux out of the head and the white area flux into the head. The arrow illustrates the location and orientation of the ECD.

were selectively averaged according to the IDI whereas responses to all standards, except those immediately after the deviant, were averaged together.

The averaged responses were digitally bandpass filtered from 0.1 to 30 Hz. Response amplitudes were measured with reference to the prestimulus baseline. N100m was defined as the maximum peak between 60 and 140 msec, and its amplitude was measured from the channel which showed the largest signal. MMFs were obtained by subtracting the response to the standard stimulus from the response to the deviant. MMF peak amplitude was measured between 100 and 300 msec.

Isocontour plots were constructed from the gradient measurements by first computing minimum norm current estimates (MNEs). Thereafter the radial field component B_z generated by the MNE was determined. This procedure accomplishes 3-dimensional interpolation suitable for the magnetic field.

If the field pattern appeared dipolar, parameters of the "equivalent current dipoles" (ECDs) that best explained the measured field patterns were determined at the peaks of the responses using a spherically symmetrical conductor model. The sphere origin was equal to that of the sphere that best fitted the head shape in the measurement area (radius 12 cm). The field maps were used only as a visual aid and the dipoles were always fitted to the original data. The fitting algorithm took into account the measured sensor locations and orientations so that the effects of primary and volume currents were properly dealt with.

Goodness-of-fit (g) values were used to determine the adequacy of the dipole model in explaining the data (Kaukoranta et al. 1986). The noise estimates for this purpose were derived from the standard errors of the means of the averaged responses; these values estimate the total experimental noise, including both instrumental noise and "brain noise" (arising from the spontaneous activity and from the variability of the signal).

We rejected from further analysis ECDs with $g <$ 85% or confidence ellipsoid volume > 4 cm^3. The 3 orthogonal axes of the confidence ellipsoid were defined on the basis of the 95% confidence limits determined along the dipole orientation, transverse to it, and in the direction of depth.

The measured data were normalized by assigning a value of 1 to the maximum N100m and MMF amplitude of each subject. Amplitudes of N100m and MMF, and the dipole moments of the corresponding ECDs were compared between conditions using 1-way repeated-measures analysis of variance.

Results

Experiment 1a – effect of number of standards

Fig. 2 shows the 24-channel magnetic signals to standards and deviants from one subject when the number of intervening standards was 19. Both responses show a prominent N100m deflection which peaks around 80 msec. The field pattern during N100m, shown in the inset, displays extrema of two different polarities, and the pattern can be satisfactorily explained by an ECD ($g = 98\%$). The dipole location agrees with earlier studies (Hari 1990) and suggests activation of the supratemporal auditory cortex.

The corresponding difference wave forms are shown in the lower part of Fig. 2. The MMF started to differ from zero at about 70 msec (i.e., during N100m) and reached its peak at 165 msec. The field pattern was dipolar during the MMF also (inset) and the ECD

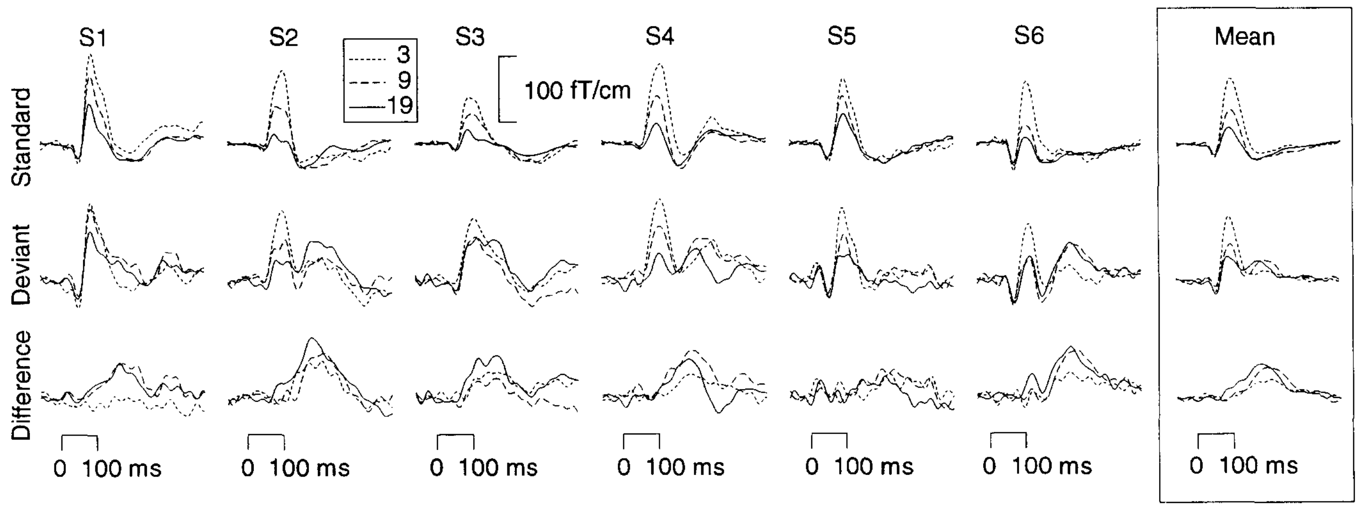

Fig. 3. Responses of 6 subjects to standards (upper row) and to deviants, which occurred at 10 sec intervals (middle row), when 3, 9 or 19 standards occurred between the deviants. The bottom row shows the corresponding difference responses. The column on the right shows the grand average of all 6 subjects.

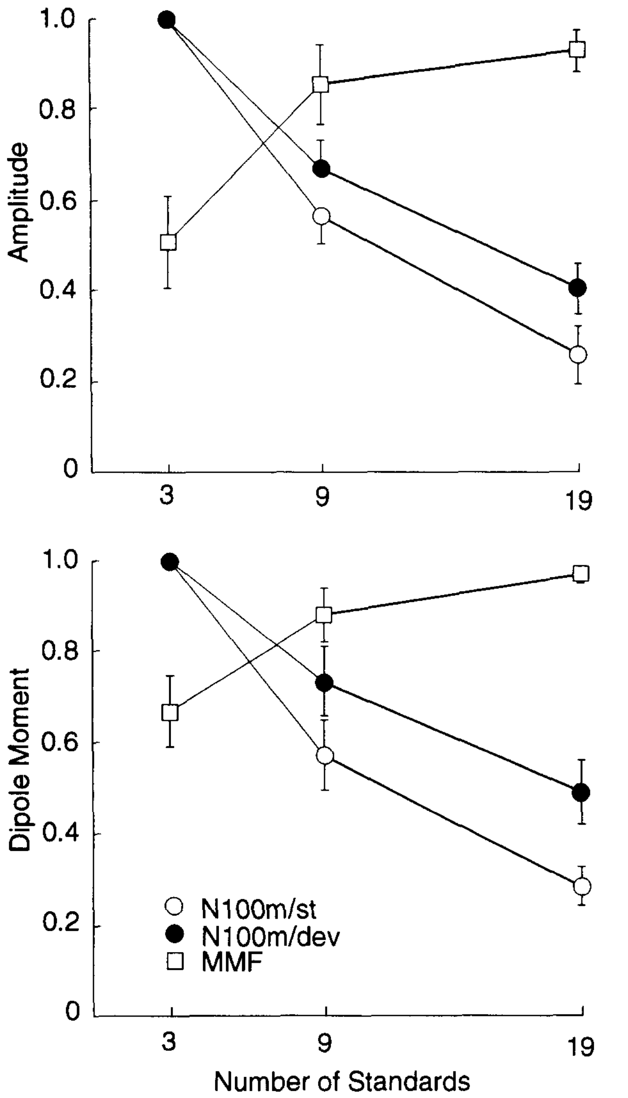

Fig. 4. Top: the mean (±S.E.M.) normalized amplitudes of N100m to standards and to deviants and of MMF as a function of the number of standards between the deviants. Bottom: the corresponding dipole moments.

accounted for 95% of the field variance. The ECD of the MMF was situated 1.5 cm superior to the source of N100m. Note, however, that the ECD locations varied as a function of time: from 70 to 90 msec the source of N100m shifted towards a more anterior location by about 1.5 cm. The source of the MMF also shifted by about 1 cm around the peak latency (150–170 msec). These shifts suggest that more than one source was active during both responses; thus comparisons at single latencies may be misleading.

Fig. 3 displays the measured MEG wave forms for all subjects from the channel which showed the largest signal. The grand average of 6 subjects is also shown. All subjects showed the largest N100m, both to standards and to deviants, with the smallest number of intervening standards. In contrast, the MMF was the smallest in this condition.

Fig. 4 shows the mean normalized N100m and MMF amplitudes, and the corresponding dipole moments. N100m to both standards and deviants decreased in amplitude as the number of intervening standards increased (standards: F (2, 10) = 95.59; $P < 0.001$; deviants: F (2, 10) = 53.23; $P < 0.001$). The standard N100m decreased by approximately 75% and the deviant N100m by 60% from the 3- to the 19-standard condition. The same effect was found for the dipole moment (standards: F (2, 10) = 80.33; $P < 0.001$; deviants: F (2, 10) = 21.79; $P < 0.001$). In contrast, the MMF increased as the number of standards increased (F (2, 10) = 5.57; $P < 0.05$), being about 40% larger in the 19- than in the 3-standard condition. The MMF dipole moment was also larger as the number of standards increased, but since the ECD model could not adequately explain the data of 3 subjects in the 3-standard condition, the data from the 3 conditions were not statistically compared.

Experiment 1b – effect of number of standards when ISI varies

Fig. 5 shows responses from two subjects who had clear MMFs to all deviants. Note the latency difference of the MMFs between the two subjects: for subject 6, the difference between standards and deviants is largest at about 230 msec whereas for subject 8 the MMF overlaps N100m. Neither subject showed systematic differences between the MMFs to the different classes of deviants. Fig. 6 shows the mean normalized amplitudes of N100m to deviants and MMF as a function of the number of preceding standards, and the corresponding dipole moments. The N100m amplitude decreased by about 30% as the number of standards increased (F (3, 18) = 20.82; $P < 0.001$). The same was

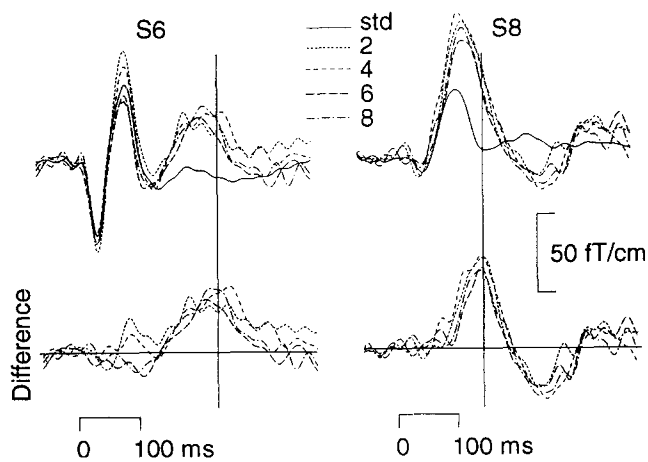

Fig. 5. The top traces show the responses of two subjects to standards (solid lines) and deviants (dashed and dotted lines). Responses to deviants were averaged according to the number of standards between deviants (2–8). The bottom traces show the difference curves. Vertical lines emphasize the latency difference between the MMFs of the two subjects.

true for the dipole moment (F (3, 18) = 6.95; $P < 0.01$). Neither the MMF peak amplitude nor the corresponding dipole moment showed a significant effect of the number of preceding standards.

Experiment 2 – effect of pISI

Fig. 7 shows the standard, deviant and difference responses of 2 subjects as a function of pISI. The grand averages are also shown. Subject 2 showed the largest N100m with pISI of 3.4 sec and the smallest with pISI of 0.6 sec. Differences are less pronounced in subject 9. The grand mean data showed the same trend as the data of subject 2. The amplitude of the MMF did not show any systematic differences as a function of pISI.

Fig. 8 shows the mean normalized N100m and MMF amplitudes and dipole moments as a function of the pISI. The amplitude of the standard N100m increased by approximately 40% while the deviant N100m amplitude increased by about 30% as the pISI increased from 0.6 to 3.4 sec (standards: F (2, 12) = 31.26; $P < 0.001$; deviants: F (2, 12) = 12.80; $P < 0.01$). The dipole moment of N100m for both standards and deviants also increased significantly with increasing pISI (standards: F (2, 12) = 16.57; $P < 0.001$; deviants: F (2, 12) = 8.97; $P < 0.01$). The MMF dipole moment decreased by approximately 20% from the 0.6 to the 3.4 sec pISI, but this effect was not statistically significant.

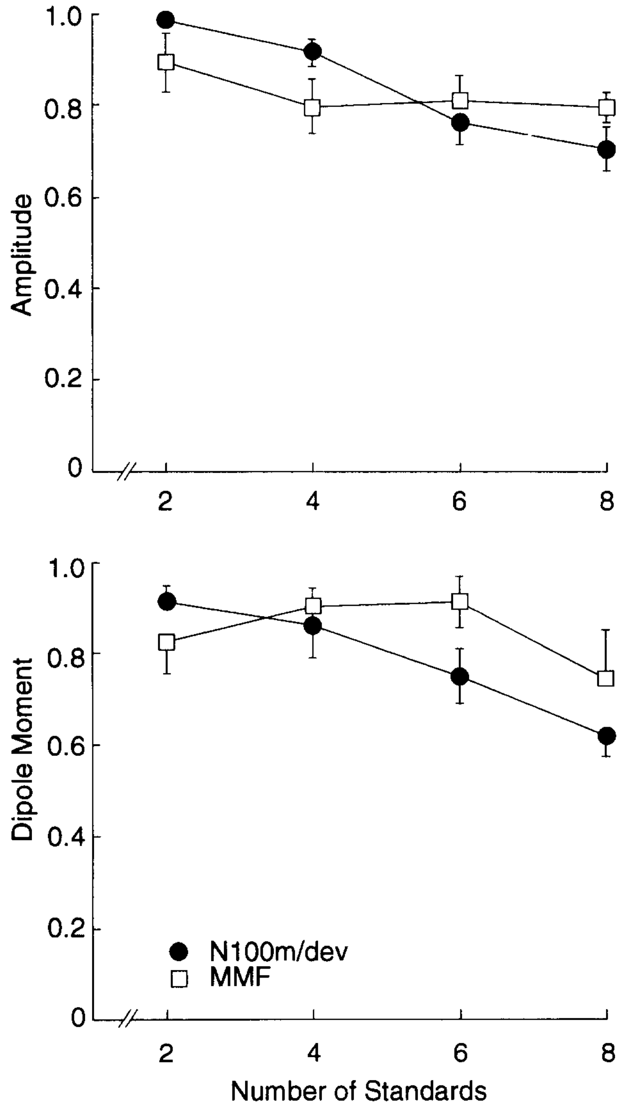

Fig. 6. Top: the mean (±S.E.M.) normalized amplitudes of the deviant N100m and of the MMF as a function of the number of standards between the deviants. Bottom: the corresponding dipole moments.

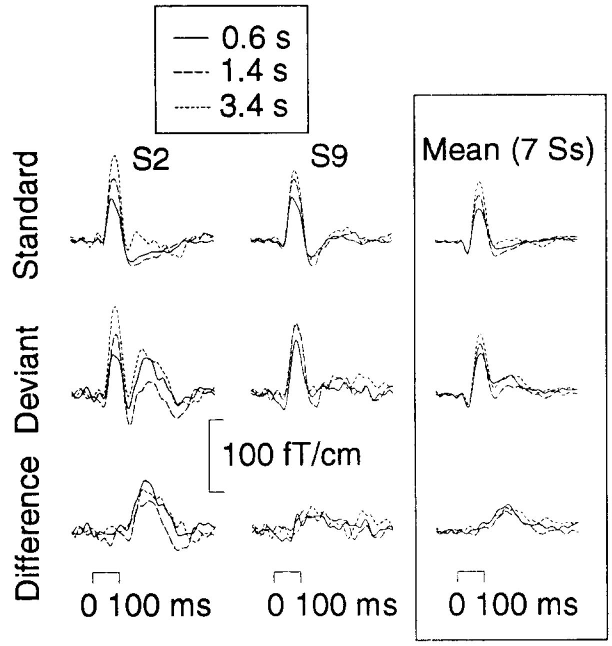

Fig. 7. The responses of two subjects to standards (top traces) and to deviants (middle traces) are shown. Standards and deviants were selectively averaged according to the pISI. The bottom traces show the difference wave forms. The right column shows the grand average traces of the 7 subjects.

Experiment 3 – effect of IDI

Fig. 9 depicts responses to the standard stimulus, the 4 classes of deviant stimuli, and the corresponding difference wave forms for two subjects. The grand average data are also displayed. Subject 4 showed clear amplitude differences between N100m to deviants presented at different IDIs, whereas for subject 13 the differences were very small. In the grand average of all 6 subjects, the deviant N100m was only slightly larger for IDIs of 6 and 8 sec than of 2 and 4 sec. Both subjects show prominent MMFs to all 4 deviants, with a tendency for the MMF to increase as the IDI increases. This tendency is also evident in the grand average data.

Fig. 10 shows mean normalized N100m and MMF amplitudes and the corresponding mean dipole moments as a function of IDI. The amplitude of N100m to deviants increased by approximately 20% between the

2 and 6 sec IDI, but the overall effect of IDI on the N100m amplitude failed to reach statistical significance. The dipole moment of N100m increased by 20% between the 2 and 4 sec IDI, then decreased. Again, the overall effect of IDI on the dipole moment was not statistically significant. The depths of the N100m dipoles in the different IDI conditions were within 2 mm of each other, and thus the variability of dipole moments cannot be due to an error in the depth estimates.

MMF amplitude was significantly affected by IDI (F (3, 15) = 4.97; $P < 0.05$), increasing by approximately 30% from the 2 to the 8 sec IDI. Although the dipole moment showed the same tendency, the magnitude of the change was less than 20%, and the overall effect of IDI was not significant.

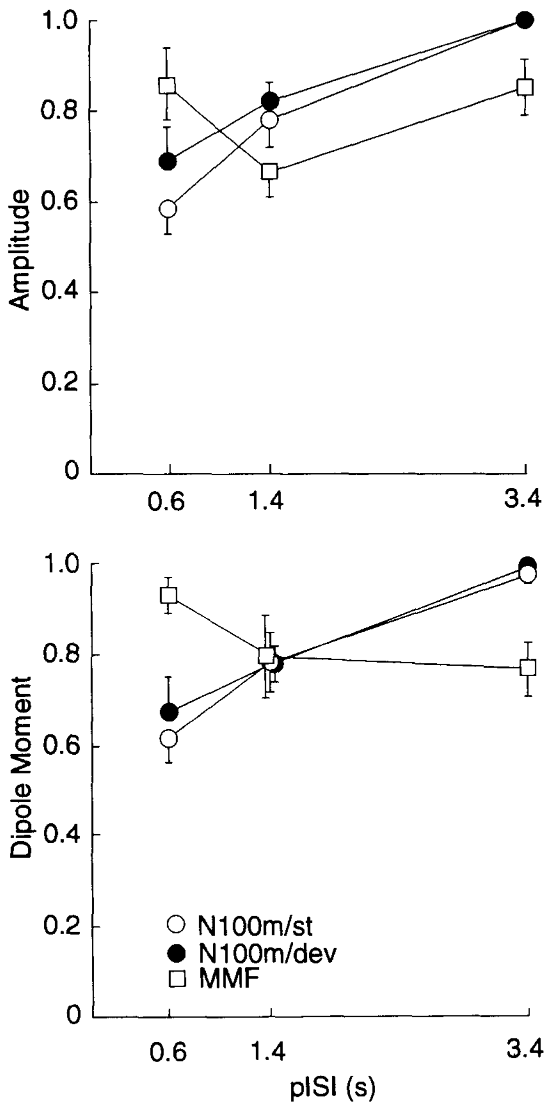

Fig. 8. Top: the mean (±S.E.M.) normalized amplitudes of the standard and deviant N100m and of the MMF as a function of the pISI. Bottom: the corresponding dipole moments.

Discussion

In an oddball experiment, a change in one of the parameters determining MMR magnitude will inevitably affect some other important parameters. For example, increasing the number of standards between consecutive deviants will either decrease ISI (if IDI is kept constant) or increase IDI (if ISI is kept constant). We tried to avoid some of these pitfalls by introducing experimental procedures in which the long-term probabilities of some parameters were kept constant. However, some of the short-term sequences were then rather complex.

The starting point of the present experiments was the assumption that the MMF amplitude is determined by the degree of mismatch between the deviant input and the trace left by the standard. In exp. 1a, MMF increased in amplitude when the number of intervening standards increased, supporting the hypothesis that the memory trace is strengthened by consecutive standards. This result agrees with the electrical results of Sams et al. (1983; see also Näätänen et al. 1987). However, in exp. 1b where ISI variability was introduced, the effect disappeared.

The different predictabilities of the deviants in exps. 1a and b most probably do not explain the discrepancy in the results since Scherg et al. (1989) have shown that predictability does not significantly effect the strength of the mismatch process. The disagreement may be understood by examining the variables that changed in each experiment. In exp. 1a, 3 parameters covaried: the number of standards between deviants, the ISI (including the pISI), and the deviant probability; only the IDI was constant. In exp. 1b, the IDI, the long-term deviant probability and the pISI were kept constant, whereas the number of standards and the ISI covaried between conditions. Two factors may therefore have contributed to the contradictory results between these experiments: the deviant probability and the temporal variability of standard stimulus presentation. The deviant probability effect does not seem plausible since in exp. 1b only the overall deviant probability was constant; there were clear short-term changes. According to Sams et al. (1993) it seems improbable that the MMF generator would have a longer "memory" than about 10 sec. This suggests that temporal variability of the standards is the crucial factor. We can account for this by supposing that the memory trace includes the temporal features of a stimulus sequence. When the single stimuli and their temporal relationships are identical, then the sequences are also identical, and standard stimuli delivered repeatedly at the same interval reinforce the memory trace for the sequence; but if the stimuli are delivered with a variable interval, then the sequence is different, and there is no reinforcement of the trace for the sequence. Existence of a memory for sequences would explain why the MMF depended on the number of standards in exp. 1a but not in exp. 1b.

In experiment 2, which was designed to test the hypothesis of memory trace decay, the MMF amplitude decreased only slightly when pISI increased. It thus seems that the memory trace does not decay enough over an interval of 0.6–3.4 sec to affect significantly the MMF amplitude. This conclusion is supported by recent MMN and MMF data (Czigler et al. 1992; Böttcher-Gandor and Ullsperger 1992; Sams et al. 1993).

In experiment 3, MMF increased as IDI increased. Simultaneously, however, the number of standards also increased, and the interpretation might thus be similar to that of exp. 1a, suggesting either a stronger trace formed by the increased number of standards or a stronger mismatch due to lower deviant probability. However, the present results do not rule out the possibility that the IDI effect could in part be due to refractoriness of the MMF generator (see Introduction).

The decrease of N100m amplitude when the number of standards increased in exps. 1a and 1b can be explained in terms of ISI variation. In exp. 1a, ISI covaried with the number of standards, increasing as the number of standards decreased. In exp. 1b, although ISI varied between 0.5 and 4.5 sec in all cases, the average ISI was longer when fewer standards occurred between the deviants. It is well known that as ISI increases, N100m increases (Hari et al. 1982, 1987; Lü et al. 1992; Sams et al. 1993). These effects can be explained by refractoriness or active inhibition of the N100m generator (Loveless et al. 1989). An expected change in the N100m amplitude was also obtained in exp. 2 where N100m increased when pISI increased. In general, N100m and MMF showed an inverse dependence on the various experimental parameters. Similar dissociation between N100m and MMR has been observed in earlier studies (Mäntysalo and Näätänen 1987; Näätänen et al. 1987; Sams et al. 1993).

Our new results demonstrate that the memory trace includes the temporal features of a stimulus sequence. A similar conclusion was reached by Nordby et al. (1988) who demonstrated an MMN to a repetition of a stimulus of a certain pitch in a sequence of two alternating sounds. A small MMN to repetitions was probably also found by Ritter et al. (1992). This adds to other evidence that the temporal ordering of a stimulus sequence is very important for the functioning of the auditory cortex. In neuromagnetic recording, such effects have been emphasized in studies using paired or tripled stimuli (Loveless et al. 1989; Hari et al. 1992; Loveless and Hari 1993) and in records of spontaneous activity (Tiihonen et al. 1991).

It seems likely that temporal features may have different effects according to the memory system involved. There is a good deal of psychological evidence suggesting that it is possible to distinguish two phases of sensory memory, a "short" phase preserving an unanalyzed auditory trace for up to 200 or 300 msec, and a "long" phase retaining more processed information for several seconds (Cowan 1984).

The short store is experienced as sensation, which persists for 200–300 msec regardless of stimulus duration and is integrated over that period. Each such segment overwrites the previous trace. This store can retain information about a brief rapid sequence of sounds but only holistically, without identifying each component. Within such a sequence, each successive sound interrupts the integration of the last. For this reason there is a decrease in the perceived loudness of

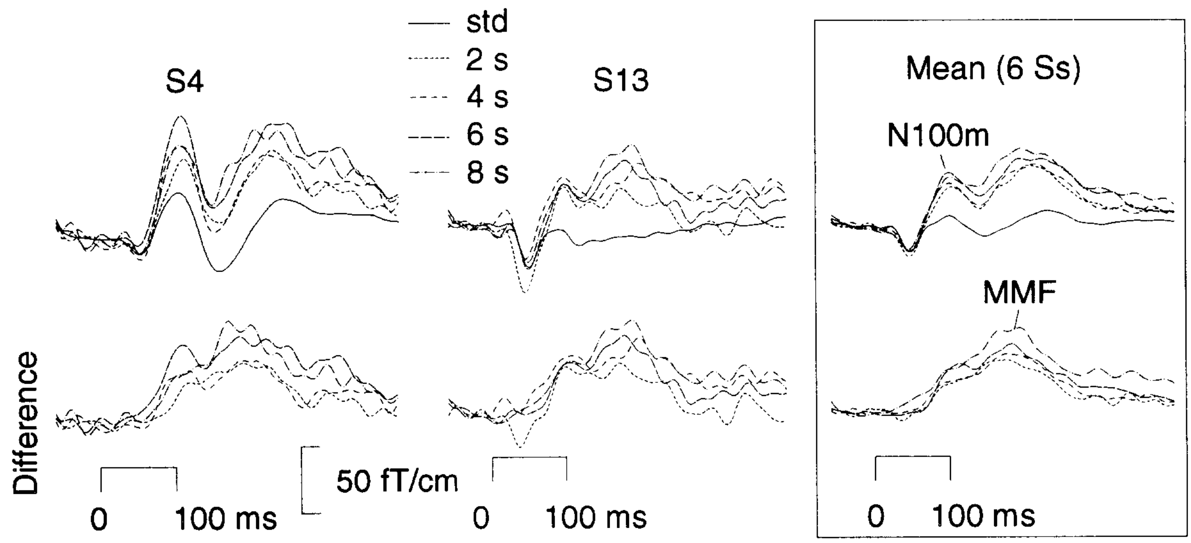

Fig. 9. Responses of two subjects to standards and deviants as a function of the IDI. The difference wave forms are shown below. On the right of the figure are the grand average traces of the 6 subjects.

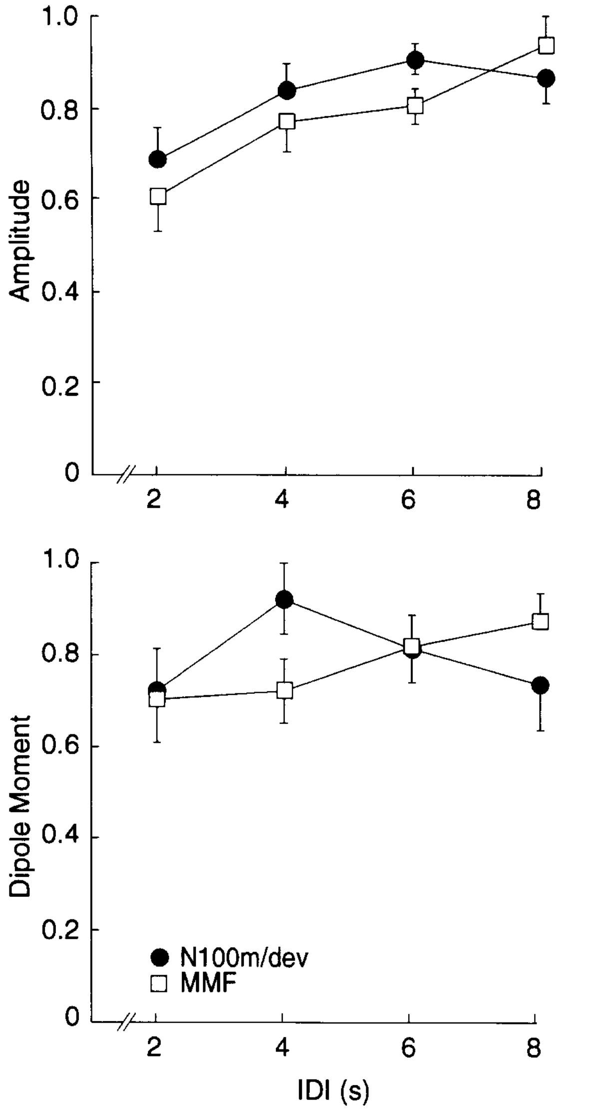

Fig. 10. Top: the mean (±S.E.M.) normalized amplitudes of the deviant N100m and of MMF as a function of IDI. Bottom: the corresponding dipole moments.

all sounds in the sequence except the last (Cowan 1987). This psychoacoustic evidence is supported by evidence from evoked responses. The N100m response evoked by the second of a pair of identical sounds differs in amplitude, latency and source location from the response evoked by the first for intervals up to 300 msec (Loveless et al. 1989, 1992).

The long phase of sensory memory is not literal and is experienced as vivid memory rather than as continued sensation. It is capable of retaining information about a sequence lasting several seconds with only partial interference. This store of more processed information permits the analysis of contextual cues and comparisons. This psychological evidence is consistent with inferences about memory systems based on data about MMR, which appears to arise from the comparison of consecutive stimuli within a time-window of about 5–10 sec. On this assumption the present results can be interpreted as follows. Decay of the memory trace is negligible during periods of 0.6–3.4 sec. Increasing the number of standard stimuli reinforces the trace but the long-term regularity of stimulus presentation is also of importance. Lack of stimulus regularity can even spoil the reinforcing effect of increasing the number of standards. The timing of the stimulus sequence is evidently preserved in this phase of sensory memory, in addition to the physical features of the stimulus. Stimuli in oddball experiments are usually presented at rates which ensure their perception as successive discrete events. The effect of repetition at such rates is evidently more complex than the refreshment of an after-image.

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