

# Magnetoencephalographic recordings demonstrate attentional modulation of mismatch-related neural activity in human auditory cortex

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## Abstract

It is widely agreed that the negative brain potential elicited at 150–200 ms by a deviant, less intense sound in a repetitive series can be modulated by attention. To investigate whether this modulation represents a genuine attention effect on the mismatch negativity (MMN) arising from auditory cortex or attention-related activity from another brain region, we recorded both the MMN and the mismatch magnetic field (MMF) elicited by such deviants in a dichotic listening task. Deviant tones in the attended ear elicited a sizable MMF that was well modeled as a dipolar source in auditory cortex. Both the MMN and MMF to unattended-ear deviants were highly attenuated. These findings support the view that the MMN/MMF elicited in auditory cortex by intensity deviants, and thus the underlying feature-analysis and mismatch-detection processes, are not strongly automatic but rather can be gated or suppressed if attention is strongly focused elsewhere.

**Descriptors:** MEG, MMN, MMF, ERP, Mismatch negativity, Attention

The occurrence of a physically deviant sound in a repetitive sequence elicits a distinctive negative component in the event-related potential (ERP) termed the *mismatch negativity* (MMN). The MMN typically peaks at around 150–250 ms poststimulus and can be elicited by deviations in a variety of auditory dimensions, including pitch, intensity, duration, location, and timing, and in more complex, patterned attributes (reviewed by Näätänen, 1992, 1995). Analyses of the neural generators of the MMN using both magnetoencephalographic (MEG) and ERP recordings have localized its principal source to the auditory cortex on the superior temporal plane (STP), with a probable secondary source in frontal cortex (reviewed by Alho, 1995). The supratemporal generators reportedly differ somewhat in position and orientation depending on the type of deviant stimulus (Giard et al., 1995). The MMN has been studied extensively as an index of basic auditory encoding and sensory memory processes in humans (Ritter, Deacon, Gomes, Javitt, & Vaughan, 1995).

Näätänen and colleagues (reviewed by Näätänen, 1992) demonstrated that the MMN can be readily elicited by deviants in an auditory sequence in the absence of active attention to that sequence (e.g., while reading). In addition, a number of researchers have found that explicit manipulations of attention failed to affect MMN amplitudes (Alho, Sams, Paavilainen, Reinikainen, & Näätänen, 1989; Alho, Woods, & Algazi, 1994; Näätänen, Gaillard, & Mäntysalo, 1978, 1980; Sams, Alho, & Näätänen, 1984). Based on these observations, Näätänen proposed that the MMN reflects strongly automatic feature encoding, memory-trace formation, and mismatch-detection processes that operate independently of attention (Näätänen, 1985, 1990, 1992).

In recent years, however, evidence has arisen to suggest that the MMN may be subject to attentional control under certain conditions. In a dichotic listening task with high sensory load, Woldorff, Hackley, and Hillyard (1991) found that the negative deflection elicited at 130–280 ms by intensity deviations in a tonal sequence was substantially reduced (by 70–90%) for tones in the unattended relative to the attended ear. The authors proposed that this deviance-related negativity (DRN)<sup>1</sup> included a MMN that was attenuated

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<sup>1</sup>The term *deviance related negativity* (DRN) is used to refer to the observed additional negativity in the deviant-stimulus ERP relative to the standard-stimulus ERP in the same channel over the interval 130–280 ms. We use DRN as a neutral term to avoid prejudging the controversial question about which functional components may be included in the overall negativity.

during highly focused selective attention to another sound source. This modulation of MMN amplitude was viewed as a consequence of an early attentional selection process that suppresses unattended inputs at the level of the auditory cortex and attenuates the earlier latency evoked components P20–50 and N1 in addition to the MMN (Woldorff & Hillyard, 1991).

In a commentary on the Woldorff et al. (1991) study, Näätänen (1991) reported that his group had confirmed that the DRN elicited by intensity deviants can be attenuated when attention is strongly focused on another auditory channel. However, he argued that the major component being modulated by attention was not actually a MMN but rather was an overlapping negativity (N2b) that is modality nonspecific and reflects the subject's detection of a potentially relevant signal. According to Näätänen (1991), the MMN can be distinguished from the N2b in scalp recordings by virtue of its polarity inversion (using a nose reference) between recording sites above and below the Sylvian fissure, which reflects its generation by vertically oriented neurons in the superior temporal plane; in contrast, the N2b reportedly does not exhibit such a polarity inversion and has an amplitude maximum over central (rather than frontocentral), midline scalp areas.

In accordance with these proposals, Näätänen and associates (Näätänen, Paavilainen, Tiitinen, Jiang, & Alho, 1993; Paavilainen, Tiitinen, Alho, & Näätänen, 1993) found that the DRN recorded over the central midline scalp to frequency-shift deviants was strongly modulated by attention during high-load dichotic listening, whereas its polarity-inverted counterpart recorded below the Sylvian fissure, which was presumed to reflect MMN activity, was not. Näätänen et al. (1993) also observed a substantial amplitude reduction of the midline DRN to intensity-decrement deviants in the unattended relative to the attended ear. In this case, however, it was difficult to determine whether the attentional modulation included an MMN according to the criterion of Näätänen (1991), because this intensity-shift DRN did not show a clear polarity reversal below the Sylvian fissure in response to either the attended or unattended stimuli. Nonetheless, because the intensity-decrement DRN elicited by the unattended-ear tones was significantly reduced relative to that elicited during a reading condition, Näätänen et al. (1993, p. 445) agreed that the MMN to intensity decrements “appears to be vulnerable to attention.”

A number of other recent studies have also reported that DRNs elicited in the 150–250-ms range by a variety of deviants are significantly larger when attention is directed toward the auditory sequence containing deviants (Alain & Woods, 1994, 1997; Alho, Woods, Algazi, & Näätänen, 1992; Oades & Dittmann-Balcar, 1995; Schröger, 1995; Trejo, Ryan-Jones, & Kramer, 1995; Woods, Alho, & Algazi, 1992.). Thus, there appears to be general agreement that the amplitude of the auditory deviance-related negative waves recorded over the frontocentral scalp can be modulated as a function of whether the auditory stimuli are being attended. What is not as clear, however, is whether these attention-related modulations of the DRN reflect a genuine attention effect on the MMN arising from the auditory cortex on the STP, in that previous studies have not included a source analysis of the attention-related change in the DRN that would help to identify its neural generators. If the DRN being modulated by attention were localized to the STP auditory cortex, for example, strong additional support would be provided for the hypothesis that the MMN generator itself can be influenced by attention. However, if that portion of the DRN originating in auditory cortex were found not to vary with attention, the proposal that the MMN itself is attention insensitive would be supported, and variation

in the DRN would then be attributable to other components such as the N2b (Näätänen et al., 1993).

In the present study, we used MEG recordings to determine the neural sources of the magnetic counterpart of the attention-sensitive DRN, which is here termed the *deviance-related field* (DRF). Previous MEG studies have shown that evoked neural activity in auditory cortical areas on the STP produces a strong dipolar magnetic field distribution over the lateral surface of the head. This field distribution has been attributed to the generator neurons being oriented perpendicularly with respect to the cortical surface (in this case, the STP) and thus tangentially to the lateral skull and scalp (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). Evoked components that have been localized by MEG to specific zones of STP auditory cortex include the M50 (magnetic counterpart of the P50), the M100 (counterpart of the N1 or N100), M200 (counterpart of the P2 on P200), and the gamma band response (Hari, 1990; Pantev, Eulitz, Hampson, Ross, & Roberts, 1996; Pantev et al., 1991; Woldorff et al., 1993). The magnetic counterpart of the MMN (i.e., the mismatch field, MMF) also arises from a tangentially oriented dipolar source in STP auditory cortex located slightly anteriorly and medially with respect to the M100 source (reviewed by Alho, 1995; Csepe, Pantev, Hoke, Hampson, & Ross, 1992; Sams, Kaukoranta, Hämäläinen, & Näätänen, 1991). In contrast, the N2b is reportedly not well registered by MEG recordings over temporal areas (Näätänen, 1990, 1991, 1995), presumably because the N2b generators either are situated outside auditory cortex or lack a systematic tangential orientation. In either case, MEG recordings during selective listening should reveal to what extent attention-related changes in this component originate from tangentially oriental sources in auditory cortex and thus may be attributed to changes in MMN/MMF.

Subjects in the present study attended selectively in a high-load dichotic listening task similar to that employed in previous ERP studies (Woldorff et al., 1991; Woldorff & Hillyard, 1991), which produced strong attentional modulation of the MMN and earlier P20–50 and N1 (N100) components. Attention effects on the magnetic counterparts of these earlier components in the present study have been described in a previous paper (Woldorff et al., 1993) in which it was reported that the sources of the early M20–50 and M100 components and their enhancements with attention were well modeled by equivalent current dipoles in STP auditory cortex. In the present report, we present the analysis of the DRFs to intensity-shift deviants recorded in the same experiment.

## Methods

MEG recordings were obtained from seven normal volunteers (ages 22–36 years) as they performed a dichotic listening task in a magnetically shielded chamber. Tone sequences were delivered through a sound-tube system and consisted of 1000 Hz tone pips to the left ear and 3150-Hz tone pips to the right ear, all of 14-ms duration with 5-ms rise and fall times. The left- and right-ear tones were presented in random order with interstimulus intervals (ISIs) ranging randomly between 125 and 325 ms (rectangular distribution). The subjects' task was to listen selectively to the tones in one ear and to detect and count occasional (9% per ear), slightly deviant tones (targets) that were 12 dB fainter than the 55 dB SL (decibels above sensation level) standard tones in that ear. All tones (both standards and deviants) in the other ear were to be ignored. The deviant tones in either ear were identical in waveshape and frequency to the standard tones in that ear, differing only in intensity. Subjects were required to make a downward movement with their

left forefinger to indicate target detections and to keep a running count of those detections.

Ten runs each of attend-left and attend-right conditions were presented in counterbalanced order. Each run lasted approximately 2 min and consisted of 250 standards and 25 deviants delivered to each ear, giving an overall total of 2,500 attended standards, 2,500 unattended standards, 250 attended deviants (i.e., targets), and 250 unattended deviants for each ear. Only responses evoked by the right ear tones (contralateral to the recording sensory array) are presented in this report.

A magnetic recording probe (Biomagnetic Technologies) containing 37 sensors spanning a circular area of 125 mm diameter was placed above the scalp overlying the left auditory cortex. A transceiver-based system was used to localize the magnetic sensory array with respect to the head. Three channels of EEG were also recorded over the left hemisphere at sites Cz, C3, and T3 (International 10-20 System) referred to the left earlobe. The recording bandpass was 0.1–200 Hz for the MEG and 0.05–250 Hz for the EEG, both of which were digitized at 861 Hz and stored on disk for off-line analysis. For each subject, averaged event-related field (ERF) and ERP waveforms were obtained to the standard and deviant tones, both when attended and when unattended. In addition, deviance-related difference waves (deviant-tone waveforms minus standard-tone waveforms) were derived for both the attended and unattended conditions. Trials contaminated with eyeblinks (as indicated by excessively large peak-to-peak amplitudes in the anterior sensors) were rejected from the averages. One magnetic sensor (no. 36) had highly elevated noise levels and was excluded from the analysis.

To quantify the deviance-related activity, mean amplitudes were measured separately for the attended and unattended standard and deviant ERP/ERF waveforms for each subject across a latency window (170–210 ms) centered over the grand-average peak deviance-related activity in the MMN/MMF latency range. These values were entered into analyses of variance (ANOVAs) with variables of attention (responses to attended versus unattended tones), deviance (responses to standard versus deviant tones) and site (sensor location). In addition, specific comparisons of amplitudes at sites around the magnetic field extrema were also conducted.

Topographic maps of the ERF distributions were calculated for the DRF and M100 peaks of the ERFs under the different attention conditions. For the M100s, mapping was carried out both for the individual subjects' ERFs and for the ERFs grand-averaged across all the subjects. For the DRFs, the topographies (and source analyses) were calculated only for the grand-averaged waveforms because the DRFs to the deviant tones, which were infrequent and fairly difficult to detect, had a signal-to-noise ratio in single subjects that was too low. For each of the surface field distributions, a best-fitting equivalent current dipole (ECD) was calculated in the MEG reference frame (a frame based on several fiducial skull landmarks), using an algorithm based on least-squares approximation (Marquardt, 1963).<sup>2</sup> As reported previously (Woldorff et al., 1993), magnetic resonance (MR) images were obtained for four of the subjects, and using the skull landmarks, the neuromagnetic reference frames for these subjects were coregistered with their MR reference frames, which allowed the ECD localization coordinates for the M100s of these individual subjects to be transposed

onto their MR images. In the present report, the neuroanatomical locations of the ECDs calculated for the DRFs were inferred from their positions in the MEG reference frame relative to the M100 ECD locations.

## Results

The distribution of the grand average ERFs across the sensor array in response to the attended right-ear tones (with standards and deviants superimposed) is shown in Figure 1; the simultaneously recorded ERPs from the C3 scalp site are shown in the upper right. The ERP waveforms included P20-50 and N100 components (peaking at 35 and 100 ms, respectively) that were elicited by both the deviant and standard tones, followed by a DRN elicited between 130 and 280 ms in response to the deviant tones only. Corresponding components could be identified in the ERF waveforms. The M20-50 and M100 components were followed by a DRF to the deviant tones that was also elicited in the 130–280-ms interval. The M20-50, M100, and DRF components all had strongly dipolar distributions, showing polarity inversions at posterior sites (e.g., Sites 22–25) in relation to anterior sites (e.g., Sites 32–35), with minimal activity at intermediate sites (e.g., Sites 3 and 4).

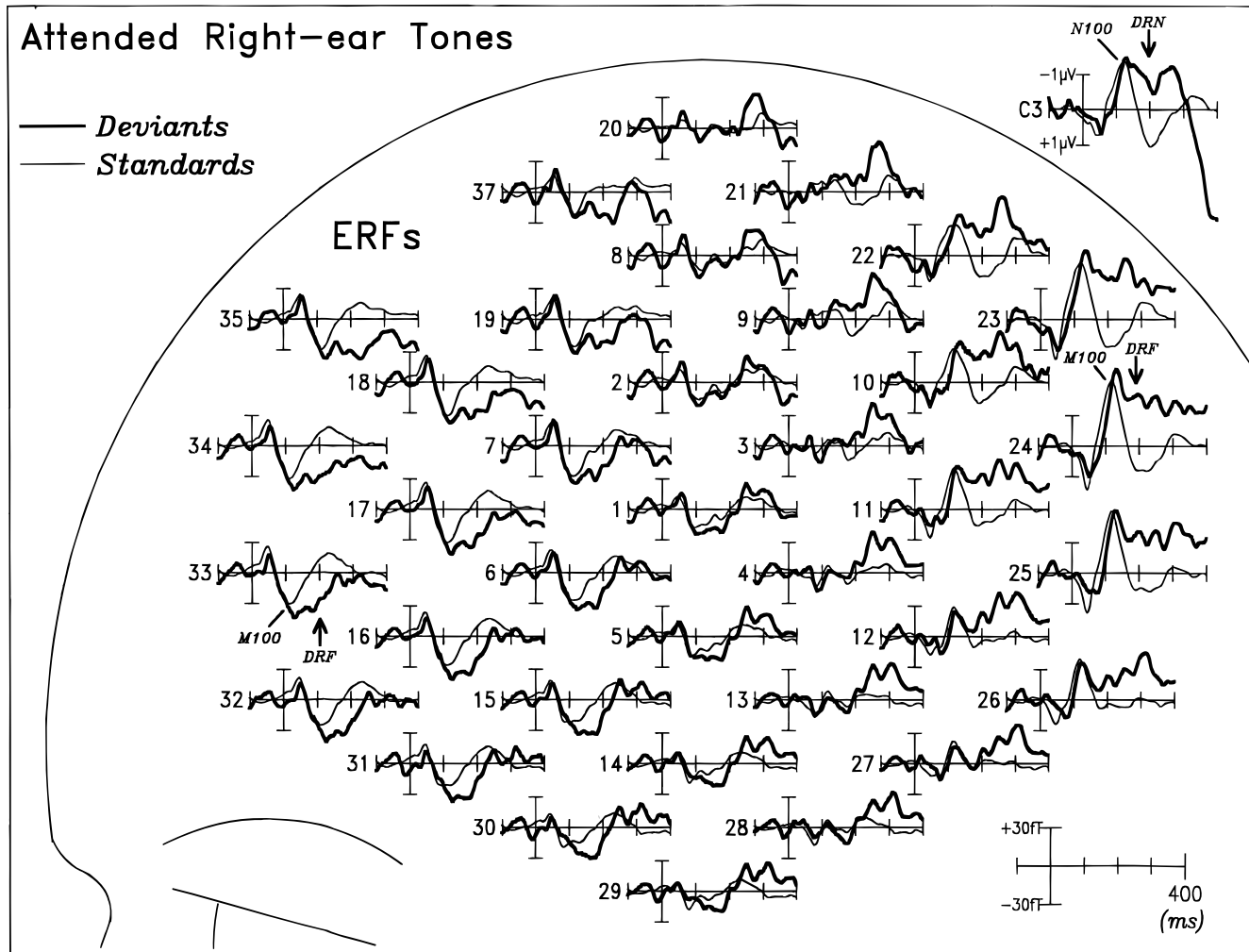
In comparison, the amplitudes of all these components elicited by right-ear tones were substantially reduced when they were unattended, that is, when the left-ear tones were attended instead (Figure 2). As previously reported by Woldorff et al. (1993), the amplitudes of the M20-50 and the M100 for the standard tones in the unattended condition (thin traces in Figure 2) were both significantly smaller than those in the attended condition (thin traces in Figure 1). In terms of deviance-related magnetic field activity, which is the focus of this report, the overlay of the unattended deviant-tone and standard-tone ERFs in Figure 2 shows a marked reduction in DRF activity in relation to that seen in the overlay of the corresponding attended waveforms in Figure 1.

The effects of attention on the deviance-related brain responses can be seen more clearly in the difference waves formed by subtracting the standard-tone response from the deviant-tone response in each attention condition (Figure 3). These difference waves illustrate that both the DRN recorded at C3 and the corresponding DRF between 130 and 280 ms were considerably reduced in amplitude (by 70–80%) when the tones were not attended. Also, the enlarged DRF to attended relative to unattended deviants is inverted in polarity at posterior relative to anterior sites, with intermediate sites showing little or no activity.<sup>3</sup> These effects are summarized in Figure 4, which compares the effects of attention on the DRN waveforms both in the present study and in the study by Woldorff et al. (1991) with the corresponding DRF changes recorded at the extrema of the magnetic field distributions. The waveforms of the DRN and the polarity inverting DRF correspond closely, with peak amplitudes at around 200 ms and with a comparable degree of attentional modulation.

Statistical analysis of the DRFs in the measurement window (170–210 ms) confirms the above observations. In the overall ANOVA, there was a highly significant Attention  $\times$  Deviance  $\times$  Site interaction,  $F(35,210) = 6.18, p < .004$ , with Huynh-Feldt

<sup>2</sup>The ECD is the single equivalent dipole source that would produce a field distribution that would best fit an observed distribution. For the dipolar distributions presented in this study, the ECD location represents the estimated centroid of the active tissue region.

<sup>3</sup>Considerable deviance-related activity was also evident at longer latencies (300–500 ms) in the attended-channel waveforms. The distribution of this late activity was more complicated than the simple dipolar fields of the M100 and early DRF, however, and appeared to involve contributions from several generators. Because this late activity was not amenable to the modeling techniques used here, it will not be considered further in this report.



**Figure 1.** Grand-averaged ( $n = 7$ ) ERF and ERP waveforms elicited by deviant and standard tones presented to the right ear in the attend-right (i.e., attended) condition. The ERF waveforms are displayed at the approximate locations of the magnetic sensors over the left hemisphere. Note the polarity-inverting deviance-related field (DRF) and M100 components at sites 24 and 33. At the upper right are the simultaneously recorded ERPs from the C3 site, showing the corresponding deviance-related negativity (DRN) and N100 components.

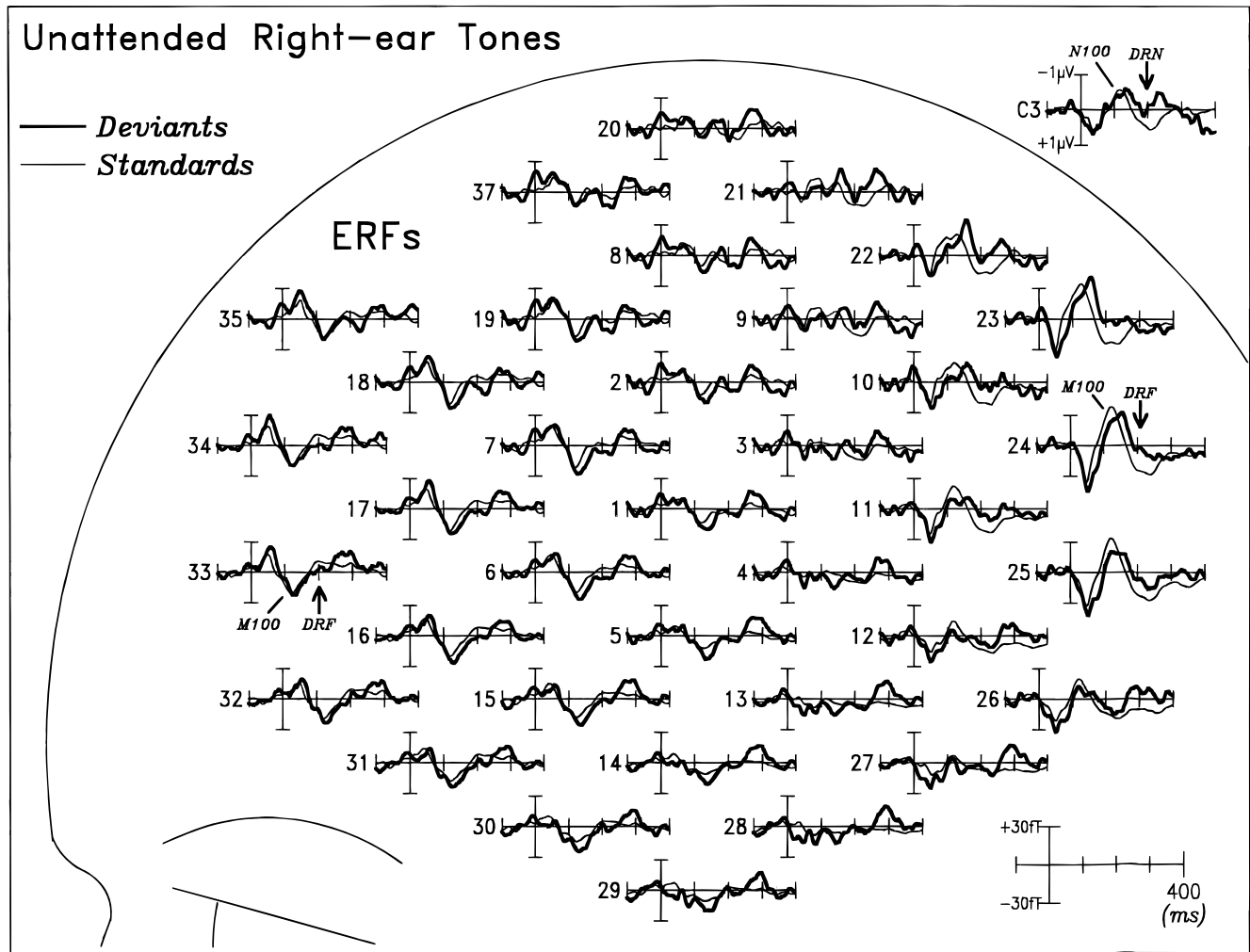
correction of  $\epsilon = 0.098$ , that resulted because the polarity inverting DRF in the attended condition was much larger than the DRF in the unattended condition.<sup>4</sup> In a subanalysis of only the attended-tone responses, the interaction of Deviance  $\times$  Site was highly significant,  $F(35, 210) = 7.85$ ,  $p < .002$ ,  $\epsilon = 0.072$ , reflecting the presence in that condition of a substantial DRF with a polarity that was opposite at anterior versus posterior sites. In contrast, in the unattended condition, the interaction of Deviance  $\times$  Site for the unattended tones did not approach significance,  $F(35, 210) = 0.91$ ,  $p < .44$ ,  $\epsilon = 0.045$ .

Specific analyses at individual recording sites around both the anterior (Sites 16, 17, 18, 32, 33, 34, 35) and posterior (Sites 10,

11, 23, 24, 25) field extrema also showed significant interactions of Attention  $\times$  Deviance ( $.005 < p < .05$ ), reflecting greater deviance-related activity in the attended condition than in the unattended condition. In addition, specific comparisons of deviant versus standard amplitudes in the attended condition alone revealed a significant DRF at these various recording sites around the extrema ( $.005 < p < .05$ ), whereas in the unattended condition the DRF was not significantly different from zero at any individual recording site.

The field distributions of the DRF in the deviant-minus-standard difference waves (cf. Figure 3) at 195 ms are shown in Figures 5A–C. The DRF in the attended condition (Figure 5A) was considerably larger than that in the unattended condition (Figure 5B), and thus its strongly dipolar field distribution closely resembled that of the DRF attention effect (Figure 5C) formed by subtracting the unattended from the attended DRF. The dipolar field distributions of both the attend-condition DRF and of the DRF attention effect strongly resembled that of the earlier-latency M100 component recorded in this experiment (Figure 5D). As previously reported by Woldorff et al. (1993), the M100 field

<sup>4</sup>This three-way interaction can be viewed as equivalent to the two-way interaction (Attention  $\times$  Site) in the ANOVA applied to the DRFs in the deviant minus standard difference waves shown in Figure 3. This Attention  $\times$  Site interaction again derives from the presence of a large DRF that inverts in polarity between anterior and posterior sites in the attended condition, with a much reduced level of such activity in the unattended condition.



**Figure 2.** Grand-averaged ( $n = 7$ ) ERF and ERP waveforms for right-ear tones in the attend-left (i.e., unattended) condition. Little DRF activity can be seen in this condition.

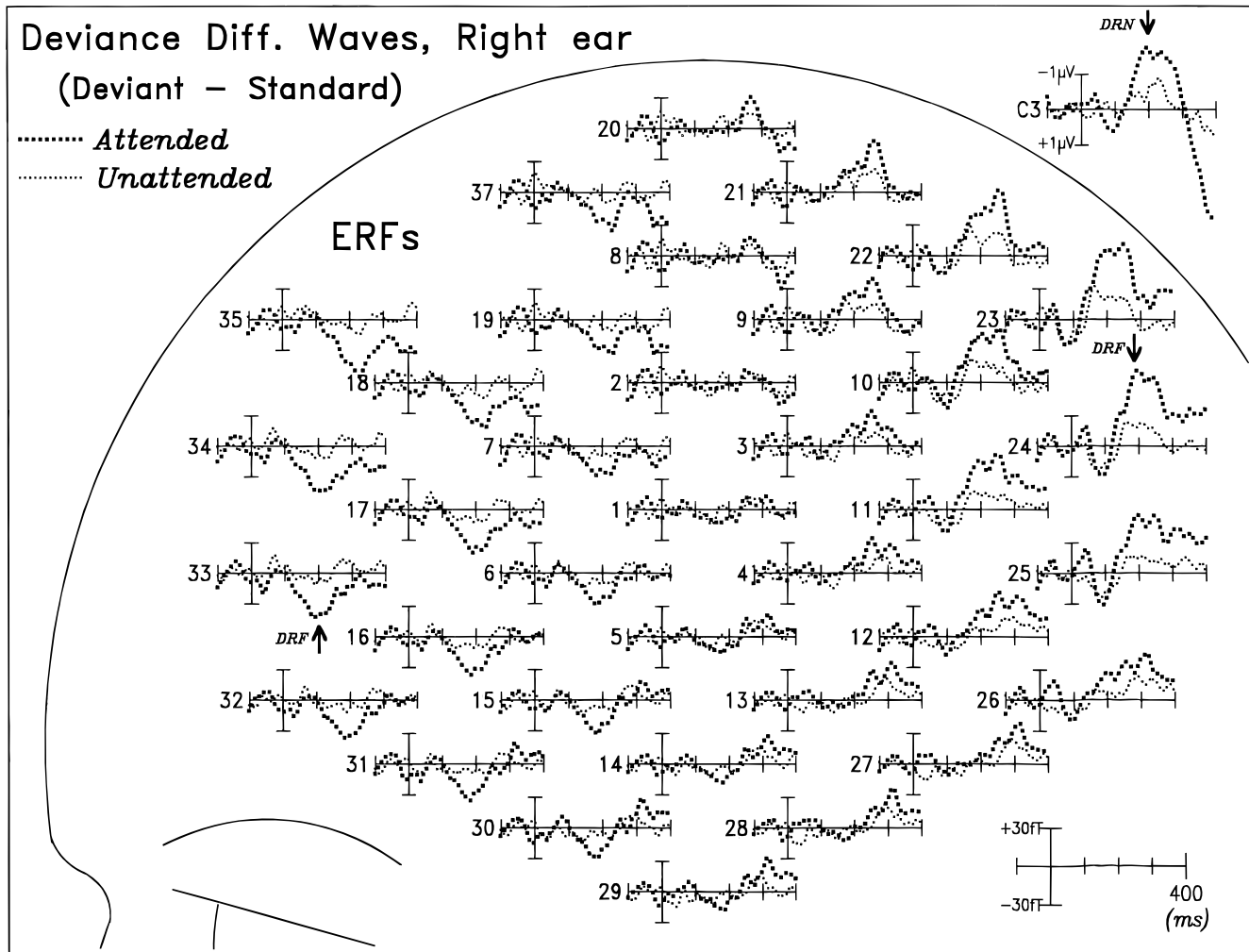
distribution was well modeled by a single dipolar source located in the auditory cortex on the superior temporal plane. The field distribution of the unattended DRF (Figure 5B) also had a generally dipolar form but with a poor signal-to-noise ratio because it was derived from a low-amplitude wave that was not significantly greater than zero.

To estimate the source location of the attention-sensitive DRF, best-fitting ECDs were calculated for the deviant-minus-standard DRF distributions shown in Figure 5. Dipole fitting was carried out only for the grand averaged DRFs (using averaged probe-placement and fiducial-landmark coordinates) because the DRFs in individual subjects had signal-to-noise ratios too low to be fit successfully using these methods. The best-fit dipoles for the attended DRF and the attended-minus-unattended difference DRF produced forward solution distributions that corresponded closely to the observed distributions (correlations of .98 in both cases). The dipole fit to the unattended DRF distribution was less precise (best correlation = .92) and was not very stable in the fitting window, as would be expected from its much attenuated amplitude. The locations of these ECDs for the grand-average DRFs are given in the  $x$ ,  $y$ ,  $z$  coordinates of the MEG reference frame in Table 1, along with the dipoles calculated for M100s. The locations for the grand-average

M100 dipoles and the mean locations of the single-subject M100 dipoles (for those 5 subjects whose M100s had good fits in all the attention conditions) are both included in Table 1 and can be seen to be in very close agreement with each other. The ECD locations for the grand-average attended DRF, the attentional difference DRF, and the grand-average M100s are displayed in the MEG coordinate space in Figure 6. The DRF dipoles were situated very near (slightly medial and anterior) to the M100 sources, which, as noted above, were localized to the auditory cortex on the STP.

### Discussion

The present results confirm previous findings (Näätänen et al., 1993; Woldorff et al., 1991) that the DRN elicited with a peak latency of around 200 ms by an infrequent intensity decrement in a repetitive tone sequence in one ear is markedly attenuated when attention is strongly focused upon a competing tone sequence in the opposite ear. Concurrent MEG recordings showed that the corresponding DRF was also substantially reduced for unattended-ear deviants such that its amplitude did not significantly rise above noise levels. This attentional modulation of the DRF (i.e., the difference between the attend-condition DRF and the much attenuated

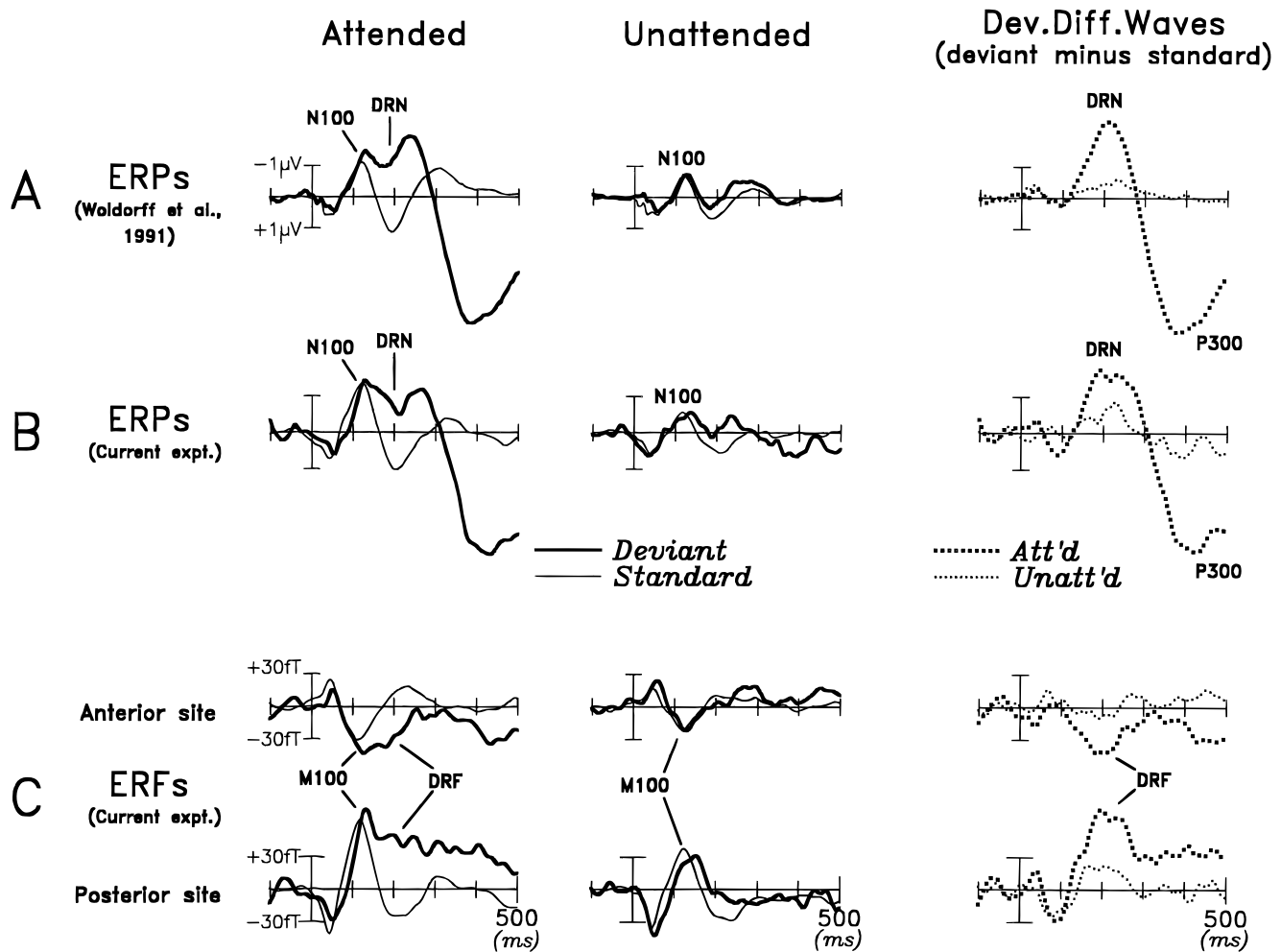


**Figure 3.** Deviance-related ERF and ERP difference waves (deviant-tone response minus standard-tone response) for the right-ear tones in the two attention conditions. These difference waveforms are derived from data shown in Figures 1 and 2. Arrows mark the polarity-inverting DRF at sites 24 and 33 and the corresponding DRN at site C3.

ated unattend-condition DRF) had a dipolar field distribution that was well accounted for by a tangential ECD located in the auditory cortex on the STP, adjacent to the dipolar source of the evoked M100 component. This localization for the DRF attention effect corresponds well with the sources that have been described for the MMN/MMF (Alho, 1995) but not with those of the N2b; Näätänen (1995, p. 11) pointed out, "the MEG does not register the N2b generator process (probably due to the radial orientation of the generator)." Accordingly, these MEG recordings provide strong support for the proposal of Woldorff et al. that strongly focused selective attention can modulate the activation of MMN generators in the auditory cortex in response to intensity-shift deviants.

An alternative possibility to consider is that the increased DRN/DRF to attended deviants includes a contribution from an increased N1 component or processing negativity (PN) associated with channel-selective attention (see Näätänen, 1991, 1992). Previous MEG studies have shown that attention effects on N1/PN do originate from tangential generators in the auditory cortex (Arthur, Lewis, Medvick, & Flynn, 1991; Rif, Hari, Hämäläinen, & Sams, 1991; Woldorff et al., 1993) and hence in principle might be con-

fusable with attention effects on the MMN. It is very unlikely that the attended deviant stimuli could elicit an enlarged PN in the present study, however, because those deviants occurred on the average only once every 5.0 s. At such a slow rate, it would be extremely difficult to maintain a distinct channel cue or attentional trace in memory for the fainter targets that would allow early selection of those targets from the much more rapidly repeating (11 times more frequent) standard tones in the attended channel. When channel cues are only reinforced at long intervals during selective listening tasks, the PN is both delayed in onset (Hansen & Hillyard, 1984) and reduced in amplitude (Alho, Lavikainen, Reinikainen, Sams, & Näätänen, 1990; Schwent, Hillyard, & Galambos, 1976). Hansen and Hillyard (1984), for example, found that the PN had an onset latency of about 100 ms when the channel cues (easily discriminable tone frequencies also separated spatially) were repeated at average intervals of 0.8 s, but the PN did not begin until after 200 ms when ISIs were lengthened to 4.0 s. In addition, previous studies (e.g., Alho, Töttölä, Reinikainen, Sams, & Näätänen, 1987; Hansen & Hillyard, 1980) have also shown that the PN is smaller and begins much later when the cues distinguishing attended and



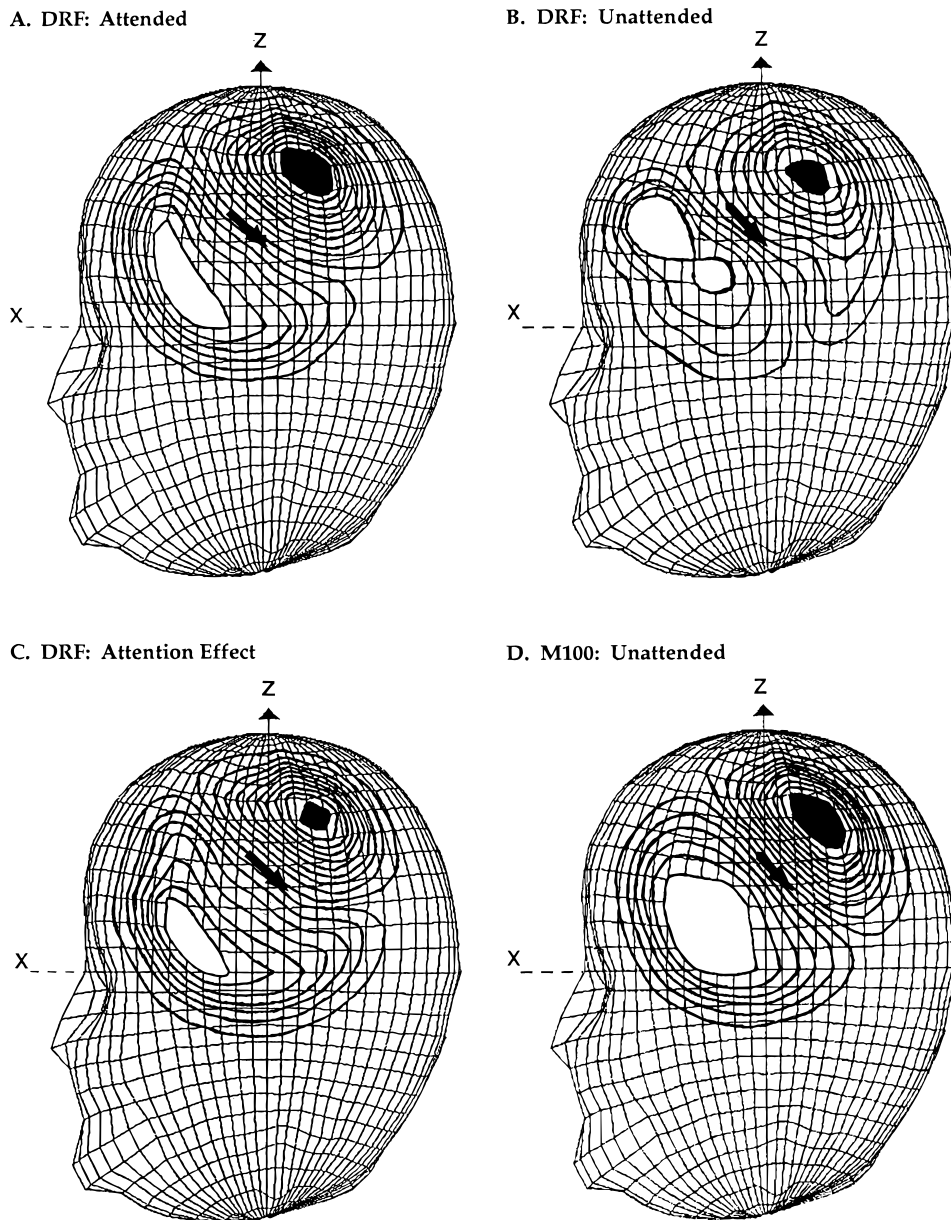
**Figure 4.** Summary of attention effects on the electrical and magnetic deviance-related responses. First two columns show grand-average ERPs and ERFs to deviant and standard right-ear tones under attended and unattended conditions, and third column shows deviance difference waves formed by subtracting the standard from the deviant waveforms. A. Data from Woldorff et al. (1991) showing strong attentional suppression of the electrical DRN at 150–250 ms (C3 site). B. Analogous data from the current experiment showing replication of attention effects on the DRN (C3 site). C. Concurrently recorded ERFs from the current experiment showing effects of attention on the DRFs recorded from an anterior site near the field minimum and a posterior site near the field maximum. Note the polarity inversion of the attention effect on the DRF and the timing coincidence of this effect with the attention effect on the DRN.

unattended stimuli are not readily discriminable, as was the case here for the rather difficult discrimination between the targets and standards. Accordingly, the sharply rising attended DRN/DRF in the present study, which onset prior to 150 ms, could not reasonably be attributed to a differential PN to the infrequent attended deviants.

Woldorff et al. (1991) interpreted the reduced MMN to intensity deviants in the unattended channel as a consequence of an early sensory gating that also attenuated evoked activity prior to the MMN including the P20-50 and N1 (N100) components. This suppression of the early components was considered to reflect a reduced flow of sensory information in the unattended channel (Woldorff & Hillyard, 1991), leading to a less effective mismatch detection process. This hypothesis of attentional suppression is consistent with the present finding that MMN amplitude was not significantly greater than zero in the unattended channel. However, in this type of design it is not possible to conclude unequivocally whether attention is acting more to enhance the MMN in the attended channel or to suppress it in the unattended channel.

Näätänen (1991) offered an alternative interpretation of this attention effect on the MMN, in line with his earlier hypothesis that the MMN reflects wholly automatic sensory analysis and mismatch detection processes. He proposed that two types of neuronal systems might be involved in MMN generation: (a) a computational system that performs the sensory analyses and generation of the mismatch signal and (b) an amplification system that augments the mismatch signal and enhances its alarming and attention-switching functions. He further suggested that attention only influences the amplification system and not the computational system, so that stimuli are fully analyzed even in the absence of attention. In this view, “the amplitude decrement (of the MMN in the unattended channel) could not be taken as suggesting that the quantity or quality of sensory information extracted from a stimulus is deteriorated by withdrawal of attention” (Näätänen et al., 1993, p. 448).

These proposals of Näätänen and associates, which would sustain the concept of strong automaticity of sensory mismatch anal-



**Figure 5.** Topographic plots (isocontour lines) of ERF distributions. Each plot is individually scaled so that distributions rather than absolute magnitudes may be compared. Note the highly dipolar field distribution, with a maximum (solid) where the magnetic field lines are directed out of the head and a minimum (open) where the magnetic field lines are directed into the head. Arrow indicates the schematic position of the single equivalent current dipole (ECD) that best fits the field distribution. A. Field distribution at the peak (195 ms) of the DRF to attended right-ear tones measured from the grand-average deviance difference waves for that condition shown in Figure 3. Isocontour scale (difference between adjacent isocontour lines) is 6.8 fT. B. Field distribution (also at 195 ms) of the DRF to unattended right-ear tones from Figure 3. This field distribution was derived for a low-amplitude wave that did not reach statistical significance. The distribution thus appears to be noisy, although it also seems to have a generally dipolar form. Isocontour scale is 2.2 fT. C. Field distribution at 195 ms of the difference between the attended and unattended DRF distributions shown in A and B, respectively. Measures were taken from the double difference waves formed by subtracting the small DRF in the unattended condition (thin dotted traces in Figure 3) from the DRF in the attended condition (thick dotted traces in Figure 3). Isocontour scale is 5.0 fT. D. Field distribution of the M100 component elicited by right-ear standard tones (unattended condition), also derived from the grand-averaged ERF waveforms. Note the strong similarity of this distribution to the attention-sensitive DRF distributions shown in A and C. Isocontour scale is 3.7 fT.

yses and MMN generation, seem debatable on several grounds. First, it seems circular to argue that an equality of MMN amplitudes in attended and unattended channels constitutes evidence for the strong automaticity of the sensory and computational analyses (e.g., Näätänen, 1992), whereas a greatly reduced MMN to unattended-channel deviants—even to the point of nonsignificance—does not weigh against such automaticity but rather is attributed to an attention effect on a separate amplification process (e.g., Näätänen et al., 1993). Following this line of reasoning, it is not clear what kind of electrophysiological evidence would be required to disconfirm the concept of strongly automatic sensory analysis. In fact, this two-stage amplification/computational model seems very difficult to test experimentally unless clear operation definitions were formulated for the hypothesized amplification and computation systems and a linkage established between those systems and sep-

arate subcomponents of the MMN. Moreover, unless these separate stages can be operationalized in terms of observables, the two-stage model is simply lacking in parsimony. The addition of a separate amplification stage to the computational stage does not seem to add any explanatory power to the model but rather acts to dissociate the physiological measure (MMN/MMF) from the information processing mechanisms of interest.

In summary, the present MEG recordings provide strong support for the hypothesis that the MMN/MMF elicited in auditory cortex by intensity-shift deviants can be suppressed by highly focused selective attention to a competing input channel. The most parsimonious interpretation of these results is that early sensory analyses leading up to and including mismatch detection are suppressed and degraded by channel-selective attention. In this view, the feature encoding, memory-trace formation, and mismatch-

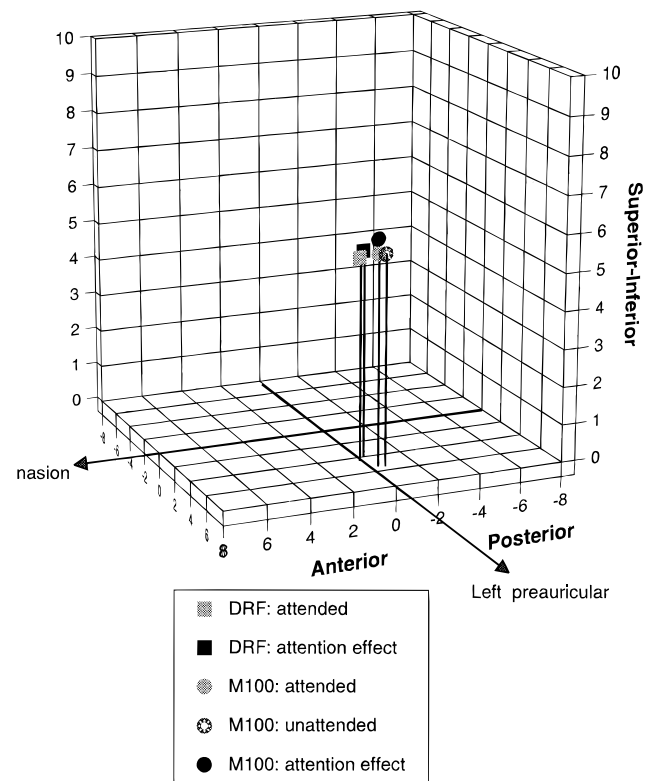


**Table 1.** Characteristics of ECDs for DRF and M100 Distributions

Condition	Latency (ms)	Fit <sup>a</sup> (%)	Angle <sup>b</sup> (degrees)	x (cm)	y (cm)	z (cm)
Grand-average DRF (n = 7)						
Attended	195	98	-122	0.1	4.4	5.5
Unattended <sup>c</sup>	195	92	-130	1.1	2.6	6.0
Attention effect <sup>d</sup>	195	98	-119	-0.2	4.0	5.4
Grand-average M100 (n = 7)						
Attended	116	98.5	-137	-0.3	5.4	5.6
Unattended	116	99	-131	-0.6	5.5	5.6
Attention effect	102	99	-141	-0.4	5.1	6.0
Mean of individuals (n = 5)						
Attended	108	98	-131	-0.7	5.5	5.8
Unattended	116	97.5	-131	-0.8	5.3	5.4
Attention effect	104	97.5	-136	-0.6	5.2	5.7

<sup>a</sup>The correlation between the measured field values and the model field values. <sup>b</sup>The orientation of the ECD dipole moment in the MEG reference frame. <sup>c</sup>The ECD fit for the unattended-channel DRF was relatively low and the locations unstable. It is nonetheless included for completeness. <sup>d</sup>Attended minus unattended.

registration processes reflected in the MMN/MMF are not fully automatic but rather are only partially automatic. In other words, these processes do not necessarily depend on attention being directed to the eliciting stimuli, but they can be suppressed or gated if attention is strongly focused elsewhere. Nonetheless, we agree with others (Näätänen, 1995; Ritter et al., 1995) that the MMN/MMF may be elicited under a wide range of conditions and attentional states and hence is a valuable tool for studying sensory encoding and memory processes.



**Figure 6.** Positions of best-fit equivalent dipoles plotted in the x, y, z coordinates of the MEG reference frame. Dipole positions are plotted for the grand-average attended DRF (solid square) and the attended-minus-unattended DRF (shaded square) derived from the distributions shown in Figures 5A and 5C, respectively. Also plotted are the M100 dipole positions from the grand-average M100 distributions: attended (solid circle), unattended (half-filled circle), attended minus unattended difference (shaded circle). Note the close proximity of the DRF and M100 dipoles.

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