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The Human Auditory Sensory Memory Trace Persists about 10 sec: Neuromagnetic Evidence

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Abstract

■ Neuromagnetic responses were recorded to frequent “standard” tones of 1000 Hz and to infrequent 1100-Hz “deviant” tones with a 24-channel planar SQUID gradiometer. Stimuli were presented at constant interstimulus intervals (ISIs) ranging from 0.75 to 12 sec. The standards evoked a prominent 100-msec response, N100m, which increased in amplitude with increasing ISI. N100m could be dissociated into two subcomponents with different source areas. The posterior component, N100m^p, increased when the ISI grew up to 6 sec, whereas the more anterior component, N100m^a, probably continued its growth beyond the 12-sec ISI. At ISIs from 0.75 to 9 sec, the deviants elicited additionally a mismatch field (MMF). The equivalent sources of both N100m and MMF were at the supra-

temporal auditory cortex. We assume that auditory stimuli leave in the auditory system a trace that affects the processing of the subsequent stimuli. The decrement of the N100m amplitude as well as elicitation of MMF can be considered as indirect evidence of active traces. A behavioral estimate of the persistence of the sensory auditory memory was obtained in a separate experiment in which the subject compared, without attending to the stimuli, tones presented at the different ISIs. The subjects discriminated the stimuli better than merely by chance at ISIs of 0.75–9 sec. The ISI dependence of the behavioral estimate as well as of N100m^a and MMF are similar enough to suggest a common underlying mechanism that retains information for a period of about 10 sec. ■

INTRODUCTION

Deeply engaged in reading your morning paper you suddenly hear your spouse demanding “What do you think of it, dear?” Fortunately, even if you have no idea of what she said to you, you can “go back in time” and give a reasonable answer. This ecologically valid behavior is based on the sensory auditory memory. Neisser (1967) described this type of “echoic” memory as the ability to “hear” a sound for some time after the physical stimulation has ceased.

Major evidence of the existence for the auditory sensory memory comes from modality-effect experiments: when sequences of auditory or visual stimuli are presented to a subject who is prompted to recall them after the last one is delivered, he remembers the last few items better if they are auditory rather than visual (Conrad & Hull, 1968; Burrows, 1972). This phenomenon suggests that auditory stimuli are kept in a sensory memory longer than the corresponding visual information.

When an extra auditory item, called suffix, is added to the end of the list-to-be-remembered, its presence effectively removes the modality effect (Crowder & Morton, 1969). This “suffix effect” is selective and it is the stronger the more the suffix physically resembles the last item of the list. However, the semantic closeness has no effect (Morton, Crowder, & Prussin, 1971). The strength of the suffix effect decreases when the time delay between the

suffix and the last item increases, thereby giving an estimate of the duration of the assumed memory trace (Crowder & Morton, 1969). Experiments with different delays have resulted in values ranging from a few seconds up to 20 sec (Crowder & Morton, 1969; Watkins & Todres, 1980).

In a backward masking experiment, a “masker” tone is presented very soon after a “test” stimulus. This results in a deteriorated detection of the test stimulus. Massaro (1972) argued that this effect is due to the preperceptual auditory storage that holds information of stimulus features necessary for recognition. If the masker occurs before the auditory information has been read out from this storage, it may erase the memory trace. The masking effect vanishes when the delay between the two stimuli exceeds 250 msec, this value providing an estimate of the maximum duration of the preperceptual auditory storage.

The estimate for the duration of the auditory sensory memory obtained from the backward-masking studies thus differs drastically from that suggested by the modality- and suffix-effect experiments. Therefore, the existence of two different auditory sensory memory systems, short and long auditory stores, has been suggested (Kallman & Massaro, 1983; Cowan, 1984). The short store, limited to 250 msec, would serve as an essential part in the auditory perception. The long store probably is a memory proper. In addition, auditory mem-

ory mechanisms of even longer duration obviously exist; we can, e.g., judge easily a single tone as high or low without any current reference tone.

The estimates of the duration of the long auditory store have varied extensively depending on the experimental paradigm (Cowan, 1984). Most studies have used verbal items that, in addition to the short and long auditory stores, probably are represented in phonetic and semantic memory stores. Many investigators have used tasks that demand active processing of the stimuli to-be-remembered, so that the different allocations of attention may explain part of the variation.

Near-threshold tones were found to be stored in the auditory memory for at least 10 sec when the subject was reading and not attending to the stimuli; he was prompted with a light cue to recall the material (Eriksen & Johnson, 1964). With verbal stimuli, likewise received without attention, Glucksberg and Cowen (1970) found a duration estimate of 5 sec whereas Cowan, Lichty, and Grove (1990) concluded that the duration of the sensory auditory memory is at least 10 sec.

Behavioral studies require an active report of the subject and the estimates therefore give indirect evidence of the duration of the memory process. We aimed at directly looking at the duration of the actual memory trace in the human brain by employing the good spatial accuracy of magnetoencephalography (MEG; for a review of the method, see Hari & Lounasmaa, 1989) to focus on the activity of the auditory cortex. We used an "oddball paradigm" in which a deviant sound is presented randomly and with low probability in a sequence of repetitive standard auditory stimuli. The deviant elicits a "mismatch response" in the human brain, detected by both electro- and magnetoencephalography (for a review, see Näätänen, 1990). Infrequent stimuli presented alone do not produce a mismatch response (Sams, Hämäläinen, Antervo, Kaukoranta, Reinikainen, & Hari, 1985; Lounasmaa, Hari, Joutsiniemi, & Hämäläinen, 1989). Therefore, a necessary condition for the mismatch response is the presence of the standards preceding the deviant and, hence, some kind of memory trace left by the standards in the auditory pathway.

The auditory stimuli elicit also an N100m¹ response (in electric recordings N100), which is likewise affected by the trace left by the previous stimuli: its amplitude is the larger the longer the interstimulus interval (Hari, Kaila, Katila, Tuomisto, & Varpula, 1982). N100m and the magnetic mismatch field (MMF) are generated in different areas in the supratemporal auditory cortex, suggesting that they reflect different aspects of the auditory information processing (Sams, Kaukoranta, Hämäläinen, & Näätänen, 1991; Hari, Rif, Tiihonen, & Sams, 1992).

Our subjects concentrated in reading and were instructed to pay no attention to the stimuli. We studied how the trace caused by the previous stimuli affects N100m elicited by a similar stimulus or MMF evoked by a dissimilar stimulus. The tones were presented at dif-

ferent interstimulus intervals (ISIs) to obtain an estimate of the trace duration. Similar stimuli and ISIs were used in a memory task to allow comparison between behavioral and neurophysiological estimates of memory trace duration.

RESULTS

Figure 1 shows a 24-channel recording of neuromagnetic responses to the standard and deviant stimuli at the 0.75-sec ISI. The responses to both sounds show a large N100m deflection, peaking at 95 msec. The later deflection, MMF peaking at 170 msec, is exclusively seen in the responses to deviants. The sensors located over the auditory cortex pick up the largest N100m and MMF. The equivalent current dipoles during N100m to the standards and during MMF to the deviants explain 98 and 78% of the field variance, respectively (MMF source was estimated from the difference waveforms where the responses to standards were subtracted from those to deviants).

Figure 2 shows responses of all subjects to standards and deviants presented at different ISIs. N100m is similar in responses to both stimuli and its amplitude grows as a function of the ISI. The responses to deviants include also an MMF starting approximately at 150 msec and often lasting until the end of the analysis period. In the mean data over all subjects, MMF is approximately equal in amplitude at three shortest ISIs. At longer ISIs, MMF becomes smaller and more variable, which is reflected in the diminished difference between the responses to the standards and deviants in the grand-averaged responses. However, subjects S2, S4, S5, and S7 show a significant (see Methods) MMF at the 6-sec ISI and the same is true for the 9-sec ISI in the data of S1, S2, S5–S7. Even at the longest ISI, four subjects (S3–S5, S7) show a significant MMF.

Table 1 shows the mean (\pm SEM) dipole parameters over all subjects for N100m and MMF. At each ISI, N100m distribution is very well explained by an equivalent current dipole (goodness-of-fit of the model \geq 97%). The source of N100m agrees with the activation of the supratemporal auditory cortex at the lower bank of the Sylvian fissure. The strength of the dipole moment depends clearly on the ISI [ANOVA; $F(5,41) = 24.8$, $p < 0.0001$]; at the longest ISI the source is more than two times stronger than at the shortest one.

The N100m latencies or the ECD locations did not change statistically significantly as a function of ISI. However, there was a trend for more anterior x -coordinates of the N100m source at longer ISIs (Table 1). A plausible explanation for this change is that there actually are two simultaneously active sources, whose relative contributions change as a function of ISI. In fact, N100m of S3 in Figure 2 shows at ISIs of 9 and 12 sec two distinct peaks. The source locations of these two components (see Methods) differed in six subjects in their x -coordinates,

Figure 1. Magnetic responses in one subject to standard (solid lines) and deviant (dashed lines) stimuli at the 0.75-sec ISI. The upper traces of each pair show field gradient along the vertical and the lower trace along the horizontal direction, indicated with arrows. The sensors located above the dipolar current source pick up the strongest magnetic signal. Approximate locations of the 24 (12 × 2) sensors are shown on the schematic head. The responses have been digitally low-pass filtered at 40 Hz.

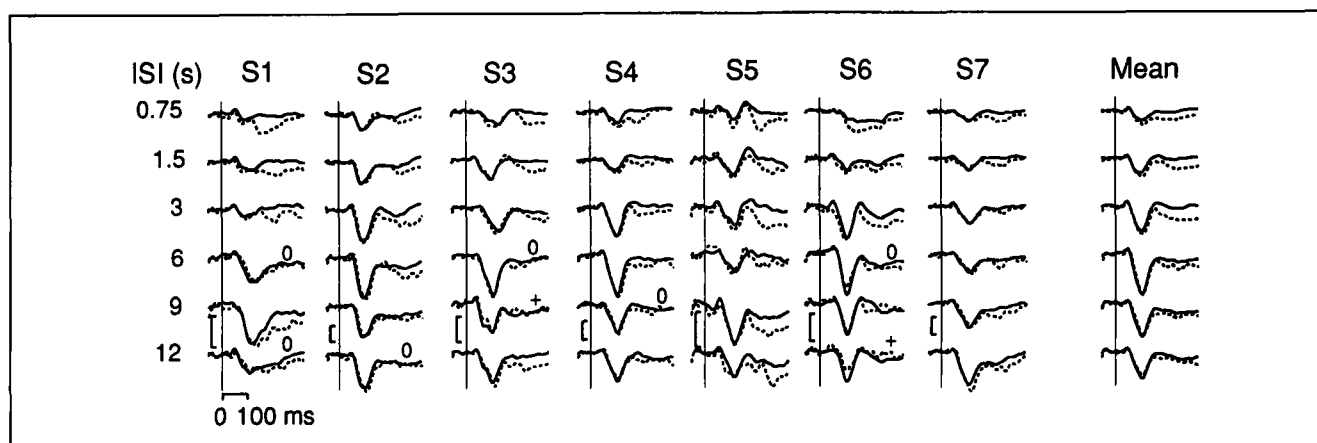
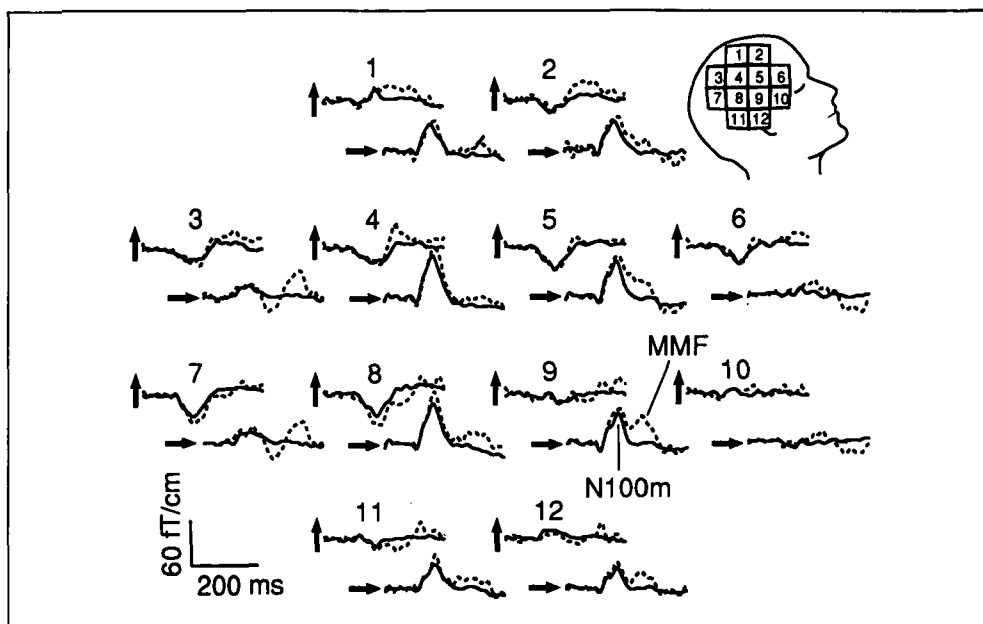


Figure 2. Magnetic responses of seven subjects to standard (solid lines) and deviant (dashed lines) tones, presented at different ISIs. The grand-average responses calculated over the subjects are shown on the right. For each subject, the signals are shown from the channel with the largest MMF at the 0.7-sec ISI. Due to pauses between sessions, responses at different ISIs were recorded from slightly different locations. Deviants showing no significant MMF are marked with 0, and those with one but of reversed polarity with +. The amplitude calibration bars are 100 fT/cm. The responses have been digitally low-pass filtered at 40 Hz. The long vertical lines show the stimulus onset.

on average by 9.3 mm [range 3.1–14.9 mm; $t(5) = 5.2$, $p < 0.005$] without any significant differences in the y - and z -coordinates. For clarity, these two components are referred to as $N100m^a$ (a for anterior) and $N100m^p$ (p for posterior).

When $N100m$ was explained by two time-varying fixed-location ECDs, the $N100m^p$ source peaked, at different ISIs, on average 29–35 msec earlier than the $N100m^a$ source. The mean goodness-of-fit values were 87–96% and 82–94% for $N100m^p$ and $N100m^a$, respectively.

The dipole moment vs. ISI dependence of the total $N100m$, $N100m^p$, and $N100m^a$ is shown in Figure 3 (see Methods). $N100m^a$ grows more slowly than $N100m^p$ as a function of ISI. This is reflected in the corresponding time constants, which are 2.6 sec for $N100m^a$ and 1.4 sec

for $N100m^p$. $N100m^p$ does not grow anymore beyond the ISI of 6 sec. However, $N100m^a$ does not seem to reach its maximum at the ISIs used. The time constant for the total $N100m$ is between those of $N100m^a$ and $N100m^p$. At the shortest ISIs, the $N100m$ deflection mainly receives a contribution from the $N100m^p$ source whereas at long ISIs, the main contribution comes from $N100m^a$; at the 12-sec ISI the mean dipole moments of $N100m^p$ and $N100m^a$ are 23.3 and 41.7 nA, respectively. Note, however, that the proportion of explained variance is low for the curve describing the ISI effect on $N100m^p$.

Figure 4a shows the effect of ISI on the dipole moment of MMF; the dipoles were calculated only when the responses of Figure 2 showed a significant MMF. This effect is significant [ANOVA; $F(5,41) = 2.9$, $p < 0.03$], due to

Table 1. The Mean (\pm SEM, $N = 7$) Peak Latencies and x -, y -, z -Locations and Dipole Moments (Q) of the Equivalent Current Dipoles for N100m to the Standards and for MMF to the Deviants at Different ISIs.^a

ISI (sec)	lat (msec)	x (mm)	y (mm)	z (mm)	Q (nA)	g (%)
N100m						
0.75	99 \pm 5	-14 \pm 2	1 \pm 1	98 \pm 1	15 \pm 2	97 \pm 1
1.5	97 \pm 3	-12 \pm 1	4 \pm 1	99 \pm 1	20 \pm 3	97 \pm 1
3	101 \pm 5	-10 \pm 3	1 \pm 1	98 \pm 1	31 \pm 4	98 \pm 1
6	100 \pm 3	-12 \pm 2	2 \pm 1	100 \pm 1	36 \pm 5	97 \pm 1
9	98 \pm 3	-9 \pm 1	3 \pm 1	100 \pm 1	39 \pm 4	98 \pm 1
12	105 \pm 5	-8 \pm 2	0 \pm 2	100 \pm 1	37 \pm 4	97 \pm 1
MMF						
0.75	202 \pm 13	-12 \pm 3	-3 \pm 2	101 \pm 2	12 \pm 1	88 \pm 2
1.5	219 \pm 17	-15 \pm 2	2 \pm 4	101 \pm 3	9 \pm 1	85 \pm 4
3	217 \pm 17	-11 \pm 2	4 \pm 2	99 \pm 3	13 \pm 2	90 \pm 3
6	210 \pm 11	-18 \pm 7	0 \pm 5	105 \pm 5	5 \pm 2	78 \pm 7
9	207 \pm 13	-12 \pm 3	9 \pm 5	97 \pm 4	5 \pm 2	78 \pm 3
12	218 \pm 16	-16 \pm 5	0 \pm 3	93 \pm 5	5 \pm 5	89 \pm 1

^aThe g -value gives the amount of field variance explained by the single-dipole model. The x -axis forms a 45° angle with a line connecting the right ear canal and the outer canthus of the right eye; it approximately follows the Sylvian fissure. The origin is 7 cm posterior to the eye corner. The y -axis points up (towards the midline) in a Cartesian right-handed coordinate system, on a plane tangential to the surface of the head. The radius of the head in the measurement area is assumed to be 120 mm; z gives the distance from the center of the sphere.

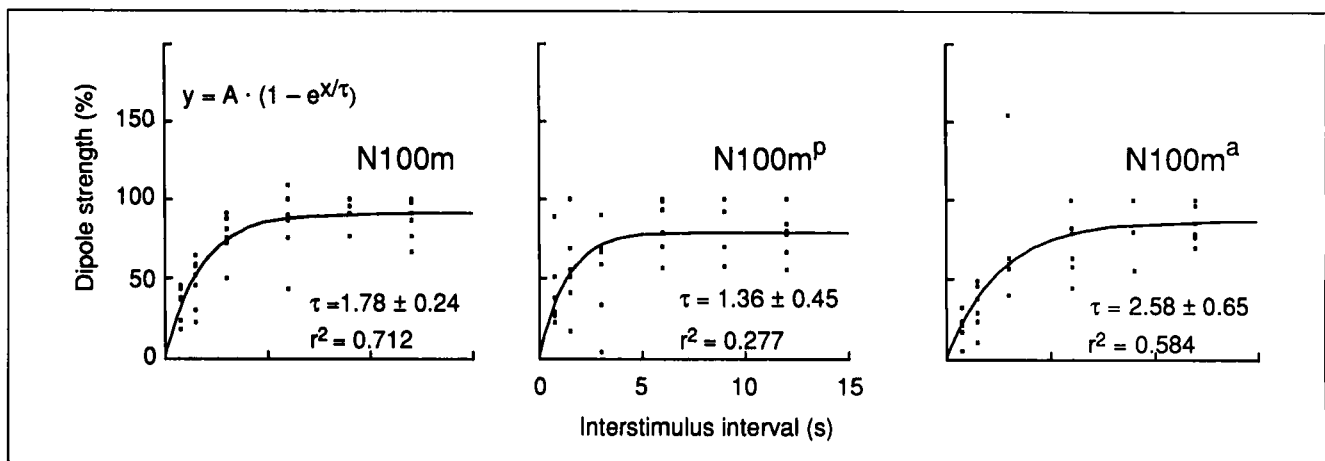


Figure 3. The normalized dipole moments of N100m, N100m^p, and N100m^a of all subjects as a function of the ISI. Time constants (τ) and proportion of the explained variance (r^2) of the fitting function are indicated.

larger values at 0.75–3 sec ISI than at those of 6–12 sec. MMF is strongest at the 3-sec ISI. A smoother ISI effect is seen in the Students t value, which describes “probability of existence” of MMF at given ISIs. The mean dipole moments differ statistically significantly from zero at the ISIs of 0.75–3 and 9 sec ($p < 0.01$, one-group two-tailed t -test) and 9 sec ($p < 0.05$). At the 6-sec ISI, MMF approached significance ($p < 0.07$).

The locations of the MMF ECDs did not differ statistically significantly at different ISIs. Neither did the ECD

locations for N100m and MMF differ significantly from each other at any ISI (see Table 1).

The mean performance in the behavioral memory test (the percentage of the subjects giving the correct answer in the tone-comparison task) is shown in Figure 4B. At the ISIs of 0.75, 1.5, 3, and 9 sec, the mean performance exceeded the chance level ($p < 0.05$, binomial test). At the 6-sec ISI, 4 of 13 subjects gave wrong answers. For the longest 12-sec ISI, the mean performance did not differ from chance level.

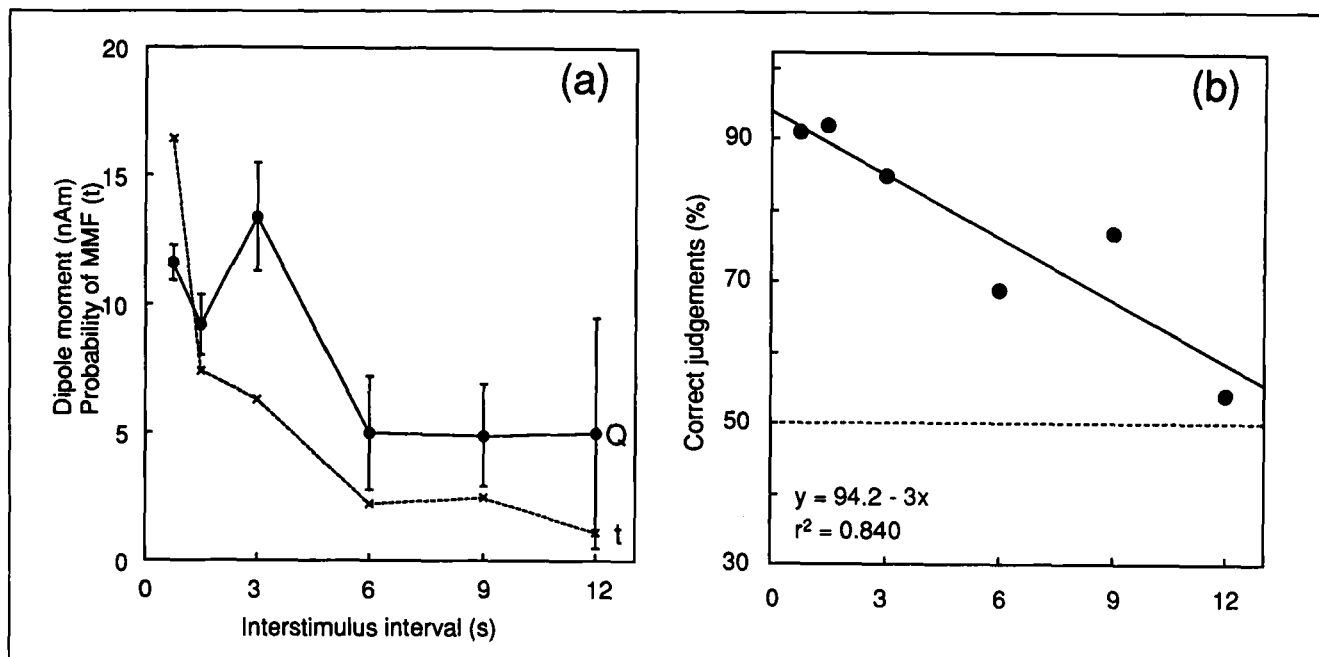


Figure 4. (a) The mean (\pm SEM) dipole moments of MMF as a function of ISI. The crosses show t values (from a Student's t test in which the significance of the deviation of the dipole moment of MMF from zero was evaluated with 6 degrees of freedom to give an impression of the "probability of existence" of MMF at different ISIs. (b) The proportion of the 13 subjects giving correct judgments in the behavioral memory task. The dashed line shows the performance level that can be obtained by chance. Data were fit to a line.

DISCUSSION

We examined the ISI dependence of the neuromagnetic N100m and mismatch responses to evaluate the lifetime of the auditory sensory memory. The study was based on the assumption that the stimuli leave a trace somewhere in the auditory pathway. When this trace is still active, it affects the processing of the subsequent stimuli. The decrement of the N100m amplitude as well as elicitation of MMF can be considered as indirect evidence of active traces.

N100m was very sensitive to the ISI as shown previously (Hari et al., 1982). However, it appeared that N100m can be divided into an anterior and posterior subcomponent, N100m^a and N100m^p, with approximately 1-cm source separation. N100m^p peaked about 30 msec earlier than N100m^a.

Lü, Williamson, and Kaufman (1992) showed recently evidence of two components in N100m deflection. Based on a two-dipole model, they suggested that one of the components originates in the primary auditory cortex and the other in the superior temporal sulcus, i.e., in the auditory association cortex. The last-mentioned "latent" component peaked about 10 msec earlier than the former one. The sources of the present N100m^a and N100m^p differed in anterior-posterior rather than in superior-inferior direction, suggesting that both sources are at slightly different areas in the supratemporal plane. A possible explanation to the discrepancy of the present sources and those of Lü et al. (1992) is that we did not allow independent variation of the sources in our two-

dipole model. This may have affected the locations of the present sources. However, the existence of two N100m components seems evident.

The spatial dissection of N100m was corroborated with a functional one showing different recovery times for the N100m components, suggesting that the trace durations differ in the corresponding areas of the auditory cortex. The time constant for N100m^a was longer, and the response seemed to grow beyond the ISIs used in the present experiment. Lü et al. (1992) also showed different ISI behaviors for these two N100m subcomponents. N100m^p reached a plateau at about 6 sec.

The deviant stimuli elicited a significant MMF at the ISIs of 0.75–3 and 9 sec and a nearly significant MMF at 6-sec ISI. Remarkably, from 0.75 to 3 sec the ISI had little effect on the strength of the MMF source. Actually, the biggest MMF was obtained at the 3-sec ISI. Recent data from our laboratory show that the MMF amplitude becomes smaller when the interdeviant interval gets shorter (Imada, Hari, Loveless, McEvoy, & Sams, 1993). This might be one reason for the strange ISI dependence of the MMF amplitude in the present study. In a similar vein, the electrical "mismatch negativity," MMN, has been found to be larger at 2-sec than at 1-sec ISI (Mäntysalo & Näätänen, 1987). The rather small effect of ISI on the mismatch response was also seen in the electric data of Näätänen, Paavilainen, Alho, Reinikainen, and Sams (1987).

Previously, Mäntysalo and Näätänen (1987) found a statistically significant MMN (standard 950 Hz, deviant 1150 Hz) at short ISIs up to 2 sec but not at 4- and 8-sec ISIs.

Näätänen et al. (1987) were able to record a significant MMN (standard 600 Hz, deviant 625 Hz) with an ISI of 4 sec; the authors did not use any longer ISIs. The present results increase the upper limit of ISI at which MMF still can be elicited to 9 sec. One reason for the different estimates might be the fact that MEG and EEG give a somewhat different picture of the cortical function. MEG is especially suitable for recording activity from fissural cortex such as the supratemporal auditory areas (Hari, 1990) whereas EEG picks up activity from the cortical areas of any orientation.

The observed sources for MMF and for both the N100m components agree with the anatomical location of the supratemporal auditory cortex (Hari, Hämäläinen, Ilmoniemi, Kaukoranta, Reinikainen, Salminen, Alho, Näätänen, & Sams, 1984; Sams et al., 1985, 1991; Kaukoranta, Sams, Hari, Hämäläinen, & Näätänen, 1989; Lounasmaa et al., 1989). However, we can not preclude the possibility that the auditory trace that underlies the ISI effect is formed on an earlier stage in the auditory pathway. In cats, "mismatch responses" can be recorded, in addition to AI and AII, in subcortical structures (Csépe, Karmos, & Molnar, 1990). Recent EEG and MEG studies suggest that the source location of MMF is more anterior than that of N100m (Scherg, Vajsaar, & Picton, 1989; Sams et al., 1991; Hari et al., 1992). However, no such difference was found in the present data. The relative locations of the ECDs for N100m and MMF may depend on several factors.

The observed ISI effects on N100m and MMF agree with results suggesting that the auditory cortex is crucial in tasks demanding delayed discrimination based on the memory of previous stimuli (Whitfield, 1985; Tramo, Bharucha, & Musiek, 1990). In cats, the auditory cortex outside AI contains neurons that are especially sensitive to changes in auditory stimuli (C. Schreiner, personal communication). Therefore, MMF might receive a contribution from the auditory belt area.

Our behavioral memory experiment suggests that auditory information persists in the attention-independent sensory memory on average for 9 sec. The better performance at shorter ISIs suggests that the memory trace weakens as a function of time. The duration estimate of 9 sec is close to those obtained in previous studies (Cowan et al., 1990; Eriksen & Johnson, 1964; Glucksberg & Cowen, 1970).

Our neuromagnetic recordings gave three different estimates for the trace duration. The shortest is that for N100m^P: about 6 sec. This is too short to explain the performance in the behavioral memory task. The ISI behavior of N100m^a suggests the trace duration of about 12 sec or even longer. The third estimate, 9–12 sec, is derived from the longest ISI showing MMFs. The last two estimates are closest to the behavioral one.

The source strengths of N100m and MMF behave like mirror images as a function of ISI; the weaker the source of N100m the stronger is that of MMF. Thus, the small

amplitude of N100m for standards and the large amplitude of MMF for deviants might reflect a strong memory trace for the standard stimulus (cf. Näätänen & Picton, 1987). Consequently, ISI effects on N100m and MMF might both reflect the memory trace underlying the results of our behavioral measurement; the duration of this sensory-specific auditory memory trace is about 10 sec.

MATERIALS AND METHODS

Neuromagnetic Recordings

Subjects, Stimuli, and Procedure

Seven healthy young adults (five males, two females) with no reported hearing disorders were studied in a magnetically shielded room (Kelhä, Pukki, Peltonen, Penttinen, Ilmoniemi, & Heino, 1982). During the measurements, the subject was lying on a bed with his head fixed with a vacuum cast. Sinusoidal sounds (intensity about 80 dB SPL, duration 50 msec including linear 10-msec rise and fall times) were presented to the subject's left ear. The stimuli were led from an earphone outside the shielded room via a plastic tube (length 3m, inner diameter 15 mm) to a nonmagnetic headphone inside the room. The frequency was 1000 Hz in 86% of the stimuli ("standards") and 1100 Hz in the rest 14% ("deviants"). The sounds were delivered at constant ISIs of 0.75, 1.5, 3, 6, 9, and 12 sec; only one ISI was used in each stimulus block. The session always started with the 0.75-sec ISI followed by other ISIs presented in random order. Several sessions, with a few short pauses between them, were run during 1–3 days.

Recording and Data Analysis

The magnetic field outside the head was measured with a 24-channel dc-SQUID (Superconducting QUantum Interference Device) gradiometer that has a low noise level of 3–5 fT/(cm $\sqrt{\text{Hz}}$) (Kajola, Ahlfors, Ehnholm, Hällström, Hämäläinen, Ilmoniemi, Kiviranta, Knuutila, Lounasmaa, Tesche, & Vilkmann, 1989). Two orthogonal loops per site measure the tangential field gradients $\partial B_r/\partial x$ and $\partial B_r/\partial y$ of the field component normal to the head, B_r , at 12 positions simultaneously. The distance between two adjacent channels is 30 mm. The pickup coils are placed on a spherical surface with a 125-mm radius of curvature; the sensors cover a 125-mm diameter cap. Such planar gradiometers give the maximum signal just above a dipolar current source.

The passband in the recordings was 0.05–100 Hz (3 dB points, roll-off for the high-pass filter 35 dB/decade and over 80 dB/decade for the low-pass filter). The magnetic signals were digitized at 1 kHz. The analysis period of 360 msec included a 40-msec prestimulus baseline and the ratio of deviants and standards in averaged responses varied from 16/83 to 71/368, respectively. The number of deviant stimuli was smaller for longer ISIs to avoid pain-

fully long recording sessions. The response to the standard stimulus immediately following each deviant stimulus was omitted from the analysis.

The exact locations and orientations of the gradiometer channels, with respect to the head, were determined by passing current through three small coils, fixed on a cap containing a coordinate grid, and measuring the elicited magnetic field with the magnetometers.

Vertical electro-oculogram (EOG) was recorded with electrodes situated just above and below the right eye; measurement epochs with EOG exceeding 150 μ V were omitted from the averages.

Parameters of an equivalent current dipole (ECD), i.e., a current dipole that best explains the measured field pattern, were determined using a spherically symmetric conductor model with a radius corresponding to the average local radius of the curvature of the head over the measurement area (120 mm). The fitting algorithm takes into account the actual measured sensor locations and orientations so that the effects of primary and volume currents are properly dealt with.

The existence of a reliable MMF in the responses shown in Figure 2 was checked by comparing responses to standards and deviants at the peak latency of MMF: MMF was regarded as significant when the amplitude difference in the responses to the standards and deviants exceeded two times the SEM for deviants (calculated during averaging). This resulted in a rather conservative estimate of the existence of MMF since the SEMs for responses to standards were smaller by a factor of about $\sqrt{5}$, due to higher number of averages.

When the signal-to-noise ratio is poor, as in the present experiment in averages to deviants at long ISIs, the dipole moment (Q) as such does not give a reliable estimate of the magnitude of the current source. Small changes in the depth may give rise to large changes in Q (Hari, Joutsiniemi, & Sarvas, 1988). To avoid this problem, we fixed the dipole depths of MMFs at 24 mm from the head surface assuming that when the ISI is varied, the dipole location remains stable but the source strength changes. To decrease the effect of noise, the dipole moment for MMF was measured as a mean over a 30-msec period from difference waveforms (responses to standards subtracted from those to deviants) digitally lowpass filtered at 30 Hz.

In the data of six subjects, N100m seemed to consist of two different components, each having its own generator source (cf. the responses of S3 in Fig. 2). From responses obtained at the 12-sec ISI, the source of the earlier component was determined at the peak of the first deflection, if present, or at the rising slope of the N100m deflection. The other source was determined 10 msec after the N100m peak. These two sources were then included in the model applying two fixed dipoles with time-varying strengths. This analysis gave dipole moments of the two components as a function of time. The effect of ISI on the dipole moments of N100m and

on its two subcomponents was explained by fitting to the data a curve $y = A(1 - e^{-x/\tau})$ where $x = \text{ISI}$, $\tau = \text{time constant}$, and $y = Q$ (cf. Lü et al., 1992). The intercept of the curve was assumed to be at origin.

Behavioral Experiment

Subjects, Stimuli, and Procedure

Thirteen young adults (12 males, 1 female) with no reported hearing disorders were studied. None of them participated in the neuromagnetic recordings. Stimuli were binaural 1000- and 1100-Hz sinusoids of 100 msec (intensity of about 60 dB SPL), delivered equiprobably through earphones. The ISIs were the same as in the neuromagnetic recordings but all ISIs occurred in a single sequence in random order. Once after each ISI type, the subject was asked to judge if the just-heard tone was similar to or different from the previous one. Such inquiries were made once in about 30 sec. The question appeared on a computer screen and was preceded by a 300-msec sequence of flashes to catch the subject's attention. The responses were stored by the computer. During the stimuli, the subjects read sexually exciting short stories, which they reported to be highly involving.

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Notes

1. In this acronym, N refers to negativity of the simultaneous electric potential at the vertex, 100 to the mean peak latency in milliseconds, and the letter "m" to "magnetic."

REFERENCES

- Burrows, D. (1972). Modality effects in retrieval of information from short-term memory. *Perception and Psychophysics*, 11, 365-372.
- Conrad, R., & Hull, A. J. (1968). Input modality and the serial position curve in short-term memory. *Psychonomic Science*, 10, 135-136.
- Cowan, N. (1984). On short and long auditory stores. *Psychological Bulletin*, 96, 341-370.
- Cowan, N., Lichteny, W., & Grove, T. R. (1990). Properties of memory for unattended spoken syllables. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 16(2), 258-269.
- Crowder, R. G., & Morton, J. (1969). Precategorical acoustic storage (PAS). *Perception and Psychophysics*, 5, 365-373.
- Csépe, V., Karmos, G., & Molnar, M. (1990). Subcortical evoked potential correlates of early information processing:

- Mismatch negativity in cats. In E. Basar & T. Bullock (Eds.), *Dynamics of sensory and cognitive processing by the brain* (pp. 279–289). Berlin: Springer.
- Eriksen, C. W., & Johnson, H. J. (1964). Storage and decay characteristics of nonattended auditory material. *Journal of Experimental Psychology*, *68*, 28–36.
- Glucksberg, S., & Cowen, G. N. (1970). Memory for nonattended auditory material. *Cognitive Psychology*, *1*, 149–156.
- Hari, R. (1990). The neuromagnetic method in the study of the human auditory cortex. In F. Grandori, M. Hoke, & G. L. Romani (Eds.), *Auditory evoked magnetic fields and potentials*, *Advances in audiology* (pp. 222–282). Basel: Karger.
- Hari, R., & Lounasmaa, O. V. (1989). Recording and interpretation of cerebral magnetic fields. *Science*, *244*, 432–436.
- Hari, R., Hämäläinen, M., Ilmoniemi, R., Kaukoranta, E., Reinikainen, K., Salminen, J., Alho, K., Näätänen, R., & Sams, M. (1984). Responses of the primary auditory cortex to pitch changes of tone pips: Neuromagnetic recordings in man. *Neuroscience Letters*, *50*, 127–132.
- Hari, R., Joutsiniemi, S.-L., & Sarvas, J. (1988). Spatial resolution of neuromagnetic records: Theoretical calculations in a spherical model. *Electroencephalography and Clinical Neurophysiology*, *71*, 64–72.
- Hari, R., Kaila, K., Katila, T., Tuomisto, T., & Varpula, T. (1982). Interstimulus-interval dependence of the auditory vertex response and its magnetic counterpart: Implications for their neural generation. *Electroencephalography and Clinical Neurophysiology*, *54*, 561–569.
- Hari, R., Rif, J., Tiihonen, J., & Sams, M. (1992). Neuromagnetic mismatch fields to single and paired tones. *Electroencephalography and Clinical Neurophysiology*, *82*, 152–154.
- Imada, T., Hari, R., Loveless, N., McEvoy, L., & Sams, M. (1993). Determinants of the auditory mismatch response. Submitted.
- Kajola, M., Ahlfors, S., Ehnholm, G. J., Hällström, J., Hämäläinen, M. S., Ilmoniemi, R. J., Kiviranta, M., Knuutila, J., Lounasmaa, O. V., Tesche, C. D., & Vilkmann, V. (1989). A 24-channel magnetometer for brain research. In S. J. Williamson, M. Hoke, G. Stroink, & M. Kotani (Eds.), *Advances in biomagnetism* (pp. 673–676). New York: Plenum Press.
- Kallman, H. J., & Massaro, D. W. (1983). Backward masking, the suffix effect, and preperceptual storage. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *9*(2), 312–327.
- Kaukoranta, E., Sams, M., Hari, R., Hämäläinen, M., & Näätänen, R. (1989). Reactions of human auditory cortex to changes in tone duration. *Hearing Research*, *41*, 15–22.
- Kelhä, V. O., Pukki, J. M., Peltonen, R. S., Penttinen, A. J., Ilmoniemi, R. J., & Heino, J. J. (1982). Design, construction, and performance of a large volume magnetic shield. *IEEE Transactions on Magnetics*, *MAG-18*, 260–270.
- Lounasmaa, O., Hari, R., Joutsiniemi, S.-L., & Hämäläinen, M. (1989). MultiSQUID recordings of human cerebral magnetic fields may give information about memory processes. *Europhysics Letters*, *9*, 603–608.
- Lü, Z.-L., Williamson, S., & Kaufman, L. (1992). Human auditory primary and association cortex have differing lifetimes for activation traces. *Brain Research*, *572*, 236–241.
- Mäntyselkä, S., & Näätänen, R. (1987). Duration of a neuronal trace of an auditory stimulus as indicated by event-related potentials. *Biological Psychology*, *24*, 183–195.
- Massaro, D. (1972). Perceptual images, processing time, and perceptual units in auditory perception. *Psychological Review*, *79*, 124–145.
- Morton, J., Crowder, R. G., & Prussin, H. A. (1971). Experiments with the stimulus suffix effect. *Journal of Experimental Psychology*, *91*, 169–190.
- Näätänen, R. (1990). The role of attention in auditory information processing as indicated by event-related potentials and other measures of cognitive function. *Behavioral and Brain Research*, *13*, 201–288.
- Näätänen, R., & Picton, T. (1987). The N1 wave of the human electric and magnetic response to sound: a review and analysis of the component structure. *Psychophysiology*, *24*, 375–425.
- Näätänen, R., Paavilainen, P., Alho, K., Reinikainen, K., & Sams, M. (1987). Interstimulus interval and the mismatch negativity. In C. Barber & T. Blum (Eds.), *Evoked Potentials III* (pp. 392–397). London: Butterworths.
- Neisser, U. (1967). *Cognitive psychology*. New York: Appleton-Century-Crofts.
- Sams, M., Hämäläinen, M., Antervo, A., Kaukoranta, E., Reinikainen, K., & Hari, R. (1985). Cerebral neuromagnetic responses evoked by short auditory stimuli. *Electroencephalography and Clinical Neurophysiology*, *61*, 254–266.
- Sams, M., Kaukoranta, E., Hämäläinen, M., & Näätänen, R. (1991). Cortical activity elicited by changes in auditory stimuli: Different sources for the magnetic N100m and mismatch responses. *Psychophysiology*, *28*, 21–28.
- Scherg, M., Vajsar, J., & Picton, T. W. (1989). A source analysis of the late human auditory evoked potentials. *Journal of Cognitive Neuroscience*, *1*, 336–355.
- Tramo, M. J., Bharucha, J. J., & Musiek, F. E. (1990). Music perception and cognition following bilateral lesions of auditory cortex. *Journal of Cognitive Neuroscience*, *2*, 195–212.
- Watkins, M. J., & Todres, A. K. (1980). Suffix effects manifest and concealed: Further evidence for a 20-second echo. *Journal of Verbal Learning and Verbal Behavior*, *19*, 46–53.
- Whitfield, I. C. (1985). The role of auditory cortex in behavior. In A. Peters & E. G. Jones (Eds.), *Cerebral cortex, Vol. 4, Association and auditory cortices* (pp. 329–349). New York: Plenum Press.