Memory Prerequisites of Mismatch Negativity in the Auditory Event-Related Potential (ERP)

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The mismatch negativity (MMN) is a component of the auditory event-related brain potential that occurs in response to infrequent changes in the physical properties of homogeneous series of sounds, even when subjects are instructed to ignore the auditory channel of stimulation. It has been proposed (e.g., Näätänen, 1990) that the MMN is generated by an automatic process in which a difference between the deviant sound and the previous, standard sound is detected by the brain. However, it is unclear how the form of memory involved is related to the rest of the memory system. The present study indicates that, for an MMN to be elicited in response to a change in tone frequency, the representation of the standard tone must be both (a) well-established as a standard in memory, and (b) in a currently active state. The relation between physiological and psychological aspects of memory representation is discussed.

A psychophysiological technique that has been used in an increasingly refined manner in recent years is the *event-related potential* or ERP: an electrical signal recorded from the scalp in a manner that is time-locked to a stimulus presentation, averaged across a large number of trials. Many researchers who record ERPs have hoped that such data could help to clarify the components of human information processing. Although considerable progress has been made in using ERPs to understand attentional processes (for a review, see Näätänen, 1990, 1992), somewhat less effort has been directed toward using ERPs to understand memory processes (see, however, Donchin & Coles, 1988; Posner & Carr, 1992).

One component of the ERP that has shown special promise as a potential index of memory processes is the *mismatch negativity response* or MMN (for a review see, Näätänen, 1990). MMN refers to a negative component of the ERP that can occur in response to a change in the physical properties of a repeated sound, even if the subject is reading and is not required to respond to the auditory channel in any way (Alho, Woods, Algazi, & Näätänen, 1992; Näätänen, Paavilainen, Tiitinen, Jiang, & Alho, in press; Sams, Paavilainen, Alho, & Näätänen, 1985). The MMN is best observed by subtracting the subject's average waveform for deviants from an average obtained for standards. In most experiments, the stimuli are simple tones and the difference between the standard and deviant eliciting the MMN is one in frequency or amplitude. (For applications to more complex stimuli, though, see Aaltonen, Niemi, Nyrke, & Tuhkanen, 1987; Ford & Hillyard, 1981; Schröger, Näätänen, & Paavilainen, 1992; Nordby, Roth, & Pfefferbaum, 1988; Sams, Aulanko, Aaltonen, & Näätänen, 1990.)

From the standpoint of memory research, the promising aspect of the MMN is that it appears to result from a mental process in which the auditory properties of the incoming sound are compared with a memory representation of the previous sounds and are found to differ from it. The empirical support for this statement rests on a distinction between two separate, but overlapping, components of the negative-going mean potential that is observed when a deviant sound is presented, MMN and N1 (see Näätänen & Picton, 1987, for a review). N1 is a component that typically peaks at 80–100 ms after the stimulus onset and occurs to standards as well as deviants. The N1 amplitude is increased when the sound contains what could be considered a new acoustic element, such as a frequency that was not present within the standard tone or an increase in the tone's intensity. The N1 response does not increase in amplitude because of what would be considered the removal of an acoustic element, such as either the omission of a single pitch that had been present in a complex tonal standard or a decrease in a standard tone's intensity. The increase in N1 to a stimulus change after a repeated, standard stimulus therefore appears to reflect a type of recovery of feature detectors that have been partially inactive for a while. In contrast, the MMN component, which typically peaks at 100–180 ms after the stimulus onset, appears to occur in response to any discriminable change in the standard, including the removal as well as the addition of acoustic elements (Näätänen, 1990; Winkler & Näätänen, in press). It may occur only if the representations of the standard and deviant sounds are discriminably different from one another (Näätänen, 1985, 1990). Thus, although N1 and MMN both are potentially relevant to memory processes, the MMN

holds promise of being most specifically relevant to the cognitive notion of a memory representation.

There is corroborating physiological evidence, from both event-related potentials and magnetoencephalography, that the N1 and MMN components are distinct from one another. The clearest evidence to date is their different scalp distributions, which presumably reflect different underlying neural generators. Specifically, the MMN has a slightly more anterior distribution than N1. Major generators of both N1 (e.g., Scherg & von Cramon, 1985) and MMN (e.g., Hari et al., 1984) are located within or near the primary auditory cortex (in the supratemporal gyri), but they are in slightly different locations (Picton, 1992; Tiitinen et al., 1992; Scherg, Vajsar, & Picton, 1989). MMN probably has a second generator in the frontal lobe (Giard, Perrin, Pernier, & Bouchet, 1990), whereas only temporal-lobe subcomponents of the N1 response have been identified (Näätänen & Picton, 1987). Thus, the MMN component of interest here can be topographically isolated in the ERP recordings.

An investigation of the preconditions necessary for the MMN to occur should help to reveal the limits on the memory comparison process that takes place while the subject is engaged in another task. One limit is that infrequent stimuli separated only by silence (i.e., in the absence of frequent standard stimuli) do not elicit the MMN component (Kraus et al., in press; Näätänen, Paavilainen, Alho, Reinikainen, & Sams, 1989). Moreover, the MMN has been obtained only after at least a few repetitions of the standard stimulus (Näätänen, 1990; Sams, Alho, & Näätänen, 1984). This suggests that a sufficiently strong memory representation of the standard might have to be formed before this representation can be successfully compared with the deviant.

Another constraint on the MMN is that the stimuli leading to the memory representation must be sufficiently recent. Mäntysalo & Näätänen (1987) found no MMN when the time between successive tones exceeded several seconds. It was assumed by these investigators that the absence of an MMN indicated that the memory trace of each tone had decayed before the end of the interstimulus interval, thus making the automatic comparison process impossible by eliminating the memory representation of the reference stimulus.

The particular type of memory representation that underlies the MMN may be important for attentional control in an information-processing perspective (see Cowan, 1990; Näätänen, 1990). Waters, McDonald, and Koresko (1977) and Cowan (1988) suggested that the operation of an attentional filter, noted long ago by Broadbent (1958), actually depends on the habituation of the attentional orienting response described by Sokolov (1963). The notion is that physically novel stimuli attract the subject's attention, thus leading to an orienting response to those stimuli (which involves both a momentary behavioral freezing of activity and an autonomic response including, for example, a slowing of heart rate, and a possible increase in perceptual sensitivity). If the novel stimulus turns out not to be important to the organism, the orienting response is inhibited after a few repetitions of the stimulus. The theoretical assumption has been that the repetitions permit a neural model of the stimulus to be constructed, after which the stimulus no longer captures atten-

tion. However, the orienting response can occur anew if there is a discriminable change in the physical properties of the stimulus (e.g., see Öhman, 1979). Therefore, the orienting response to stimulus change is assumed to depend on a mismatch between the neural representation of previous stimuli with each successive stimulus. Notice that this is the same assumption that is made in the case of the MMN. In both cases, there must be a well-formed (through repeated presentation) neural representation of a standard stimulus for a response to a change to be elicited.

One seemingly odd aspect of the hypothesis that the subject must develop a representation of the standard stimulus is that, in the case of MMN research, the standard typically has been a simple tone. One might have expected that this stimulus is known well to the subject and that repeated presentations of the standard tone would not be needed to develop a memory representation adequate for detecting the change to a deviant tone. However, there are at least two reasons why repeated presentation might be needed. First, the representation of a single standard might decay or drift quickly over time (see Cowan, 1984, for a review of studies revealing auditory memory decay across a period of several seconds). This memory decay seems to be especially likely given that the sounds are to be ignored; memory for sounds ignored while reading is known to decrease steadily across several seconds (Cowan, Lichty, & Grove, 1990; Eriksen & Johnson, 1964). It is possible that repetitions of the standard tone somehow make its memory representation resistant to decay.

Second, it may be that the critical memory representation is not the representation of a single tone, but that of the total acoustic environment across time. Within that environment, repetitions of a tone indicate that it is the norm or, literally, the standard. It is only within the context of repetition that the deviant stimulus can be viewed as a departure from the norm. Why, according to this account, would the MMN not be obtained when the intertone interval is longer than several seconds (Mäntysalo & Näätänen, 1987)? It could be because the memory of the standard has decayed over time, or perhaps because the interval changes the context, which signals that the previous norm is no longer applicable.

To date, the MMN appears to be the clearest electrophysiological index of a memory comparison process per se, independent of shifts of attention that might follow a change in memory representation (Näätänen, 1990). However, before the MMN literature can be of use in understanding the physiological bases of memory, a bridge between MMN and the cognitive concept of memory representation is needed. It must be demonstrated that the memory of the standard stimulus is a representation that has to be developed even when the standard is a simple tone.

One way to demonstrate that MMN depends on a memory representation is to apply the concept of memory *reinstatement* or *reactivation*, which might be defined as the use of a relatively brief presentation to renew the effects of a previous, more extensive presentation. Rovee-Collier and Hayne (1987) reviewed various types of research demonstrating this phenomenon and described Rovee-Collier's finding that, when infants learned to carry out a simple action

to move a mobile and then evidenced forgetting over the course of some days, the memory still could be reinstated by a brief presentation of the mobile. This implies that the memory of the original learning persisted in some form but entered a dormant state until its reinstatement. Analogously, if there is a memory representation of the standard tone in the MMN procedure, then it should be possible to put that representation into a dormant state through the imposition of a silent period, and then to reinstate the memory of the standard with a reminder presentation. The goal of the present study was to test this prediction of a memory-representation hypothesis of MMN.

The present two-part hypothesis, which states that an MMN can occur only if (a) a stable memory representation of the standard has developed and (b) the memory representation is in a currently active or contextually relevant state when the deviant is presented, leads to some straightforward predictions. It takes several presentations of the tone for a memory representation marking it as standard to develop. However, if a standard representation has been formed but has entered a dormant state, a single presentation of the standard might suffice to reinstate it.

In the present study, these predictions were tested in a procedure in which a tone of a deviant frequency was presented in Position 1, 2, 4, 6, or 8 of a nine-item train of standard stimuli, with 610 ms between tones in a train and 11–15 s between trains. The latter time period eliminates the MMN when imposed between all tones in a series (Mäntysalo & Näätänen, 1987). In a constant-standard condition, the frequencies of the standards and the deviants were fixed throughout the session, which permitted a memory representation of these tones to carry over from one train to the next. In a roving-standard condition, however, the frequencies of the standards (and deviants) changed between stimulus trains, so that much less useful representations could be assumed to have developed over the session.

Method

Subjects

Twelve normal, young adults (5 women and 7 men, aged 19–33 years) served as subjects. Each was a member of the laboratory research staff or a student at the University of Helsinki. All had served previously in ERP experiments, but were naive about the hypotheses of the present study.

Stimuli and Procedure

The acoustic stimuli, which were generated by a custom-designed, software-controlled oscillator, consisted of tones (sine waves) with a duration of 55 ms, including 2.5-ms rise and fall times. Tones were presented monaurally to the subject's right ear at a constant, comfortable listening level (76 dB) through an electrically shielded Sony headphone held in place by the headset.

Subjects brought their own reading material and were to read it during the session and ignore the tones. Subjects were also instructed to avoid unnecessary eye movements and blinking during the session. Each subject participated in four sessions on separate days, with each session lasting about 3 hr. Two of the four sessions

were for the constant-standard condition, and the other two were for the roving-standard condition. Half of the subjects received the constant-standard sessions first, and the other half received the roving-standard sessions first. Each session included six blocks of stimuli, with breaks as needed between the blocks.

Each stimulus block lasted about 20 min and included 60 sequences of 9 tones (540 tones per block in all). There was a 610-ms interval between the onsets of tones in a sequence. Between sequences, the silent (offset to onset) interval lasted 11, 12, 13, 14, or 15 s. Within a tone sequence, 1 tone could be deviant in frequency. The deviant was either 1st, 2nd, 4th, 6th, or 8th of the 9 tones, or there was no deviant at all in the sequence. Within a block, each of these six possibilities occurred 10 times (twice followed by each of the five possible intersequence delays). Within both the constant- and the roving-standard conditions, there were 12 different random orders of the sequences in a block, thus making up the 12 blocks per condition. Subjects received the blocks within each condition in a counterbalanced order.

In the constant-standard condition, the standard-tone frequency was always 600 Hz and the deviant-tone frequency was always 700 Hz. In the roving-standard condition, however, the standard-tone frequency was fixed within a sequence but differed from one sequence to the next. The frequencies of the standard and deviant tones in a sequence could be 420 and 490 Hz, respectively; 465 and 543 Hz; 510 and 595 Hz; 555 and 648 Hz; 600 and 700 Hz; 645 and 753 Hz; 690 and 805 Hz; 735 and 858 Hz; or 780 and 910 Hz. Notice (a) that the ratio of the frequencies of the deviant to the standard in a sequence was always 7:6 (a nonharmonic ratio), the same as in the constant-standard condition, and (b) that the mean frequency across all of the different standards and deviants was equal to the respective frequencies in the constant-standard condition. The possible frequency pairs were randomly distributed among sequences, with the restriction that no two consecutive sequences could have the same frequency values.

Data Recording Apparatus

The experiment was conducted in an electrically shielded, sound-attenuated room. Responses were recorded with Ag/AgCl electrodes. Electrodes were placed in accordance with the conventional ("10–20") system in midline prefrontal (Fpz), left frontal (F3), midline frontal (Fz), right frontal (F4), midline central (Cz), and midline parietal (Pz) recording sites. An additional electrode was placed at the left mastoid (LM) under the left ear, and the reference electrode was attached to the nose. The rationale for these last two electrodes was the prior finding of an inverted MMN at the mastoids (e.g., Novak, Ritter, Vaughan, & Wiznitzer, 1990), which made it useful as one signature of the MMN but inappropriate as a reference electrode. Electrooculograms (EOGs) were recorded with an electrode situated over the outer canthus of the right eye (horizontal EOG right, HEOG-R). The bandpass region for electroencephalogram (EEG) recording was 0.1–100 Hz (−3 dB points). The analysis epoch for all channels was 500 ms, which included 50 ms before and 450 ms after the onset of each stimulus.

Data were recorded with a PDP 11 computer and transferred to a Vaxstation 3100 computer for averaging. The first 10 epochs of each stimulus block were omitted from the analysis, as were epochs contaminated by blinks, eye movements, or muscle artifacts exceeding a threshold of ±75 μV at any electrode, all of which were assumed to reflect contamination from extracerebral sources.

Data Reduction

Within each block of sequences, average ERPs were calculated for each type of deviant (i.e., deviants in Positions 1, 2, 4, 6, and

8), as well as for standards that were in the same sequential positions and were preceded by homogeneous series of standards (with which responses to the deviants can be statistically compared). Average ERPs also were calculated for standards in Positions 3 and 5 preceded by homogeneous series of standards. A researcher who was not one of the present authors examined the average ERPs for each block of data and, without access to the conditions from which they originated, marked certain blocks for exclusion on the basis of excessive directional bias in the eye movements across trials. Approximately 3% of the blocks were rejected in this manner. The remaining blocks contributed to the average ERPs for each subject that entered into the various statistical analyses. These average ERPs were then bandpass filtered with 1.6–30 Hz, to exclude baseline shifts and high-frequency noise.

Statistical analyses were conducted using the BMDP software package (Dixon, 1985). For those cases in which analyses of variance (ANOVAs) with repeated measures were conducted, the Geisser-Greenhouse correction was applied as is appropriate for correlated successive measures.

Results

Identification of MMN Responses to the Deviant

Grand average ERPs to standard and deviant tones presented as the second or fourth stimuli of the sequences in each condition are shown in Figure 1 to illustrate the response pattern for each recorded electrode location. In this and subsequent ERP figures, negative potentials are plotted upward from the baseline. In broad terms, the mismatch response is the extra negativity in response to deviant tones (thick lines) in comparison with standard tones (thin lines) in the range of about 80–200 ms. However, at least when the magnitude of the stimulus change is substantial, this extra negativity is composed of two overlapping components: the N1 response enhancement and MMN response (Novak et al., 1990; Sams et al., 1985; Scherg et al., 1989).

On the basis of previous research findings (e.g., Giard et al., 1990; Paavilainen, Alho, Reinikainen, Sams, & Näätänen, 1991) the F4 location (i.e., the right frontal locus) was assumed to provide the best estimate of MMN. (It has been suggested by Giard et al., 1990, and by Näätänen, 1990, that this lateralization of the MMN may be related to its function as an attention-recruiting signal.) At this location, therefore, the mean of the difference between ERPs to deviants and standards was calculated in the MMN range (100–180 ms) for each sequential position in which deviants occurred.

The (deviant–standard) right frontal (F4) difference waves for each condition and serial position are shown in Figure 2. In the constant-standard condition (left column of the figure), one can see that the deviant produced extra negativity starting in Position 2. In the roving-standard condition (right column), on the other hand, this extra negativity did not emerge until Position 4.

Dependent t tests were carried out for each condition at each serial position to confirm these observations and to compare the mean ERP amplitude in response to the deviants (in the 100–180-ms interval) with that of the standards in the same serial position. In the constant-standard condition, the mean ERP amplitude was significantly more negative for the

deviants in Positions 2, 4, 6, and 8: Position 2, $t(11) = 4.56$, $p < .001$, $SE_M = 0.22$; Position 4, $t(11) = 3.41$, $p < .006$, $SE_M = 0.14$; Position 6, $t(11) = 3.99$, $p < .003$, $SE_M = 0.16$; Position 8, $t(11) = 3.21$, $p < .009$, $SE_M = 0.24$. However, the result for Position 1 did not approach significance, $t(11) = 1.12$, $p > .25$, $SE_M = 0.52$. In the roving-standard condition, significance was obtained in Positions 4 and 6: Position 4, $t(11) = 3.74$, $p < .004$, $SE_M = 0.18$; Position 6, $t(11) = 3.46$, $p < .006$, $SE_M = 0.25$; and the result in Position 8 approached significance, $t(11) = 1.73$, $p = .11$, $SE_M = 0.28$. However, the result did not approach significance for this condition either in Position 1, $t(11) = 0.19$, $p > .85$, $SE_M = 0.41$, or in Position 2, $t(11) = 0.46$, $p > .65$, $SE_M = 0.21$.

It is clear from Figure 1 that much of the change across positions was a decrease in the response to the standards rather than an increase in the response to the deviants. Thus, in the roving-standard condition, the response to the standard can be seen to have decreased markedly from Position 2, in which there was no significant MMN, to Position 4, in which there was an MMN. However, there are two reasons why it can be concluded that the deviant–standard difference wave negativity was not totally due to habituation of responding to the standard tone across positions. First, notice that almost as much habituation of responding to the standard tones between Positions 2 and 4 took place in the constant-standard condition, even though there was a significant MMN of comparable magnitude at both of these positions.

Second, we conducted analyses that demonstrated that the habituation of responding to the standard was distributed across electrodes differently than was the mismatch response. In these analyses, standard stimulus habituation at any position i was measured by subtracting the average response to standards at position i (with no deviant in the preceding sequence) from the response to standards at Position 1. The magnitudes contributing to the analyses were each subject's mean responses in the 100–180-ms measurement period, the same as for the mismatch responses. A different distribution across electrodes of the habituation-to-standard component and mismatch component should result in a Component × Electrode Location interaction. However, for each subject, the habituation-to-standard and the mismatch scores were separately converted to z scores before being entered into analyses to avoid interactions that are based on differences in scale. The analyses included data from all positions at which a mismatch response was obtained (Positions 2, 4, 6, and 8 for the constant-standard condition and Positions 4, 6, and 8 for the roving-standard condition).

For each condition, an ANOVA of habituation-to-standard by mismatch response was conducted using all of the midline electrodes (Fpz, Fz, Cz, and Pz), and another was conducted using a left-to-right array of frontal electrodes (F3, Fz, and F4). The mean z scores for all combinations of condition, component, and electrode location are shown in Table 1. More negative means reflect both greater habituation and a larger mismatch response. The means suggest that habituation to the standard was more centrally distributed than the mismatch response. The mismatch response was more diffuse across electrodes and was more frontally located; unlike the habituation-to-standard response, the mismatch response
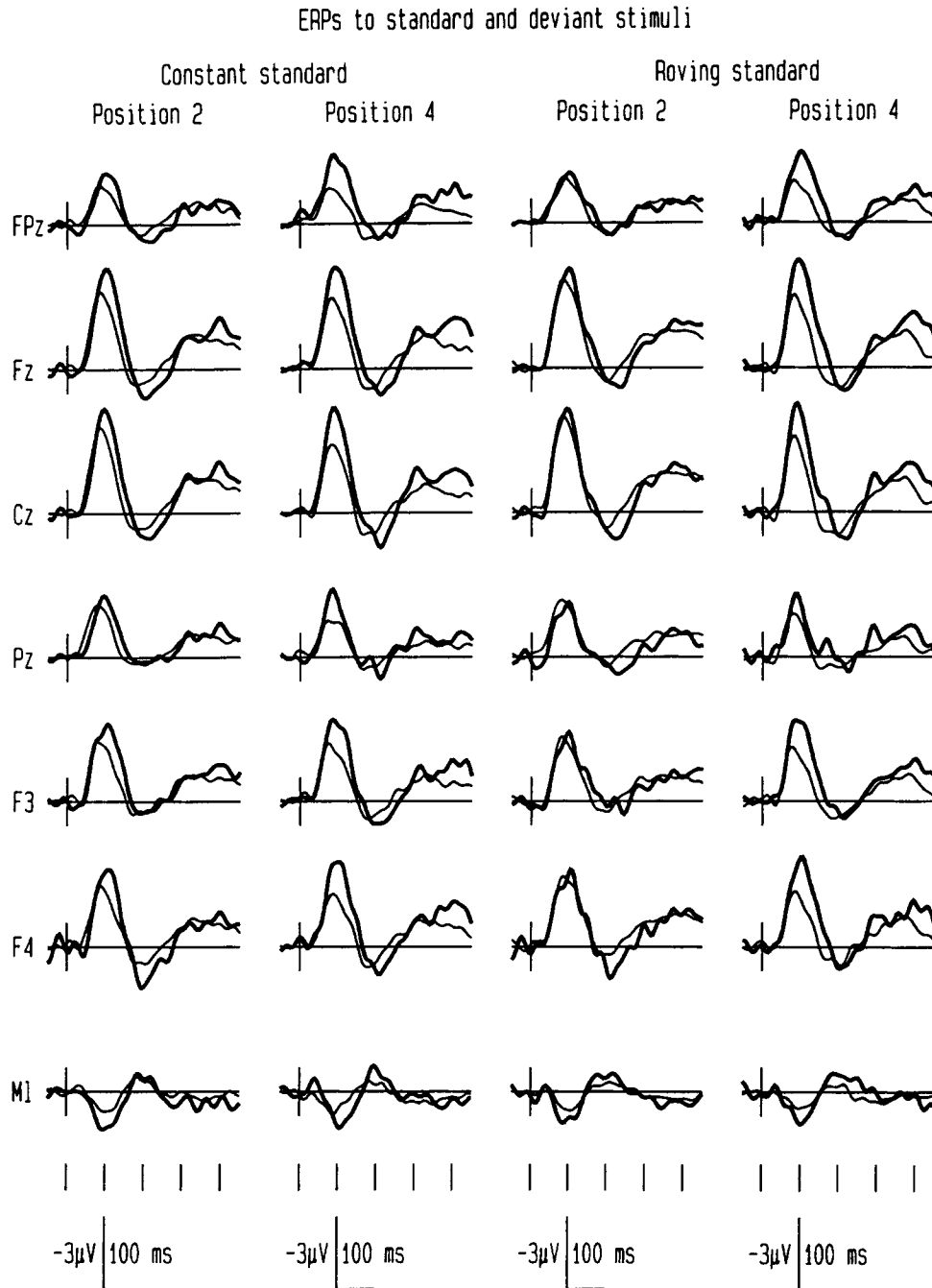
ERPs to standard and deviant stimuli

Figure 1. Across-subject-averaged event-related potentials (ERPs) to standard (thin line) and deviant (thick line) stimuli at each electrode location in the constant-standard condition (first column, Position 2; second column, Position 4) and in the roving-standard condition (third column, Position 2; fourth column, Position 4). (The two positions were selected to best illustrate the difference between the results of the two conditions. Negative values appear above baseline, and positive values appear below.)

included considerably more negativity at Fz than at Cz. This is to be expected if the deviant–standard difference is predominantly the MMN, whereas the generator of the habituation to the standard is related to the N1 response, because MMN is more frontal than N1 (Näätänen, 1990).

In support of this pattern shown in Table 1, the interaction of Component × Electrode Location was significant in all four analyses: of the midline electrodes in the constant-standard condition, $F(3, 33) = 6.64$, $p < .02$, $MS_e = 0.86$, and in the roving-standard condition, $F(3, 33)$
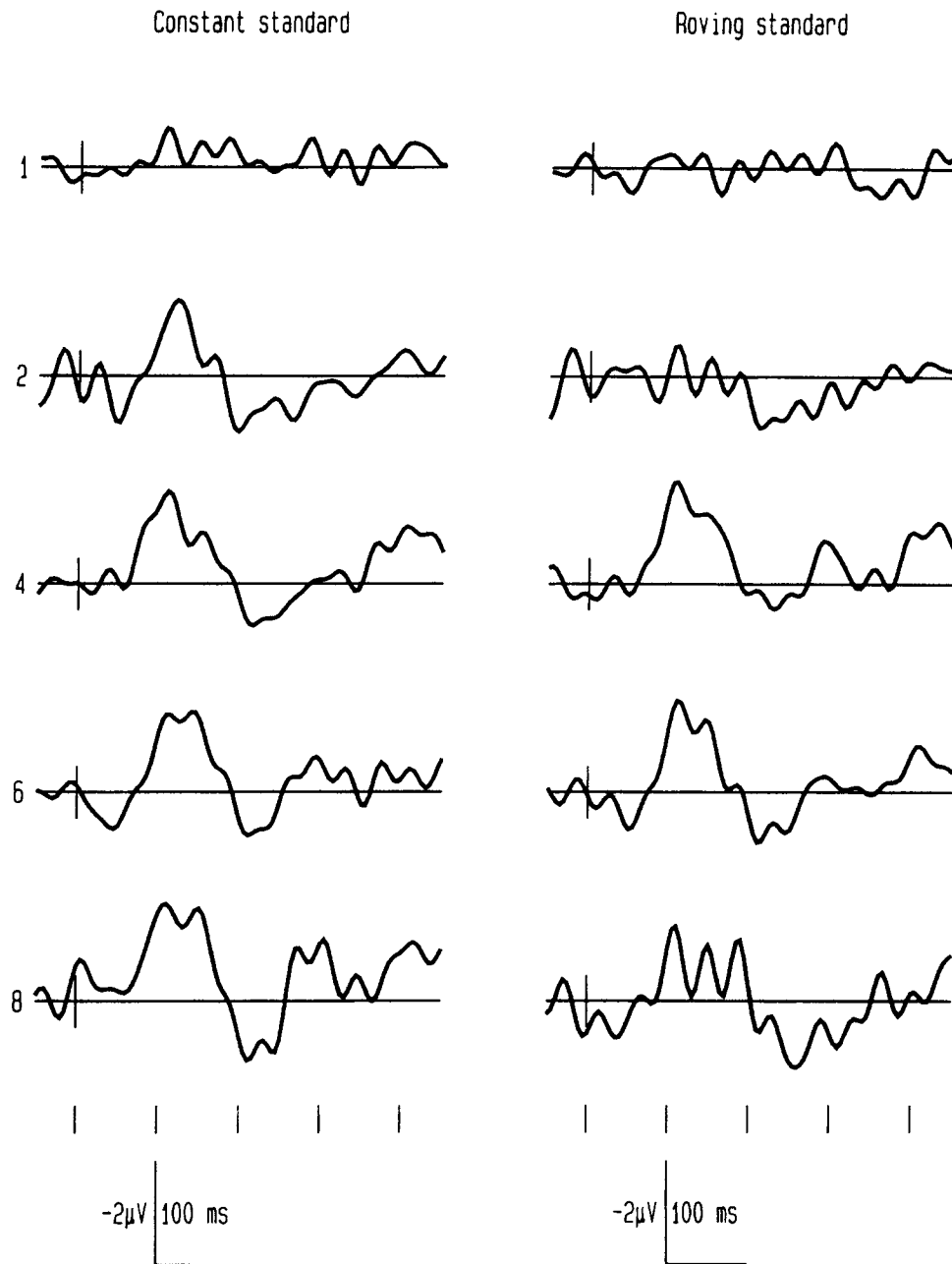
Difference curves from F4 between ERPs to
deviant and standard stimuli

Constant standard   Roving standard

-2μV 100 ms   -2μV 100 ms

Figure 2. Across-subject-averaged mean difference waves between event-related potentials (ERPs) to deviant and standard stimuli for each position at which a deviant could occur, in the constant-standard condition (left column) and in the roving-standard condition (right column). (Negative values appear above baseline, and positive values appear below.)

= 14.69, $p < .001$, $MS_e = 0.36$, and of the frontal lateral-line electrodes in the constant-standard condition, $F(2, 22) = 5.41$, $p < .02$, $MS_e = 0.40$, and in the roving-standard condition, $F(2, 22) = 7.16$, $p < .02$, $MS_e = 0.42$.

These effects indicate that habituation of the response to the standards could not totally account for the mismatch response, which makes it more likely that MMN was present.

Table 1

Across-Subject-Averaged Mean Habituation-to-Standard and Mismatch Response Amplitudes (in Microvolts) at Each Electrode in Each Condition

Electrode	Component	
	Habituation to standard[a]	Mismatch response[b]
Constant-standard condition		
Midline		
Prefrontal (Fpz)	0.74	0.17
Frontal (Fz)	-0.79	-0.46
Central (Cz)	-0.70	-0.23
Parietal (Pz)	0.75	0.52
Frontal lateral line		
Left (F3)	0.36	0.10
Midline (Fz)	-0.52	-0.19
Right (F4)	0.17	0.10
Roving-standard condition		
Midline		
Prefrontal (Fpz)	0.88	0.24
Frontal (Fz)	-0.83	-0.51
Central (Cz)	-0.71	-0.16
Parietal (Pz)	0.66	0.43
Frontal lateral line		
Left (F3)	0.47	0.17
Midline (Fz)	-0.80	-0.34
Right (F4)	0.33	0.17

Note. Across-subject-averaged z scores, normalized separately for habituation-to-standard and mismatch negativity (MMN) components for midline and frontal lateral-line analyses. The positions included in these means are those displaying an MMN to the deviant: Positions 2, 4, 6, and 8 for the constant-standard condition and Positions 4, 6, and 8 for the roving-standard condition. Means include data across a 100–180-ms window. [a] Average (Standard 1 − Standard i) event-related potential difference, where i = any position at which a mismatch response occurred. [b] Average (Deviant i − Standard i) event-related potential difference.

Pattern of MMN Responses Across Conditions

For both conditions, Figure 3 illustrates the mean values from the (deviant–standard) difference waves in the 100–180-ms range for the electrode (F4) that the literature suggests most clearly reflects the MMN. Clearly, this difference wave (which we take to reflect the MMN) displayed a different pattern in the two conditions. Neither condition displayed the MMN at Position 1, only the constant-standard condition displayed the MMN at Position 2, and both conditions displayed the MMN by Position 4.

The data were statistically analyzed in several ways. First, planned t-test comparisons between MMN amplitudes measured from identical serial positions in the two conditions were carried out. They revealed a significant difference only at Position 2, $t(11) = 2.40, p < .04, SE_M = 0.21$. As shown in Figure 3, an MMN was elicited by deviants in the constant-standard condition after only one presentation of the standard. In the roving-standard condition, no MMN was elicited by deviants presented as the second stimulus of the sequence. On the other hand, a series of three stan-

dards apparently was enough for a subsequent deviant to elicit the MMN component.

Several ANOVAs on the mismatch responses also were carried out. First, an omnibus ANOVA of all mismatch responses, with condition (constant, roving), serial position (1, 2, 4, 6, and 8), and electrode location (Fpz, Fz, Cz, Pz, F3, and F4) as within-subject factors yielded significant effects of serial position, $F(4, 44) = 5.51, p < .005, MS_e = 3.59$, and electrode location, $F(5, 55) = 7.27, p < .001, MS_e = 0.89$, as well as a Position × Electrode interaction, $F(20, 220) = 2.73, p < .02, MS_e = 0.25$. All of the relevant means are shown in Figure 4. As Figure 4 illustrates, the mean mismatch response increased across positions and was larger for frontocentral electrodes. The basis of the interaction appears to be that the increase in negativity across positions (presumably reflecting the establishment of the MMN) was weaker in the Fpz (extreme frontal pole) and Pz (parietal) electrodes than in all of the other electrodes.

No effect involving condition was significant in this omnibus ANOVA, but we attribute that to a lack of power for investigating modestly sized higher order effects. Responses at Position 2, averaged across electrodes, differed markedly in the constant-standard condition, $M = -0.93 \mu V$, versus the roving-standard condition, $M = -0.34 \mu V$. In fact, at Position 2 there was no overlap in the distribution of mean scores among the six electrodes in the constant (-0.63 to $-1.22 \mu V$) versus roving (0.01 to $-0.59 \mu V$) conditions.

As mentioned earlier, F4 is considered to be the clearest index of the MMN response. Serial position effects were investigated for this electrode more powerfully, in separate one-way ANOVAs of mismatch responses for each condition with position as a within-subject variable. The analysis for the constant-standard condition resulted in a significant effect of position, $F(4, 44) = 3.64, p < .03, MS_e = 0.56$. Post hoc (Neuman-Keuls) pairwise comparisons indicated that
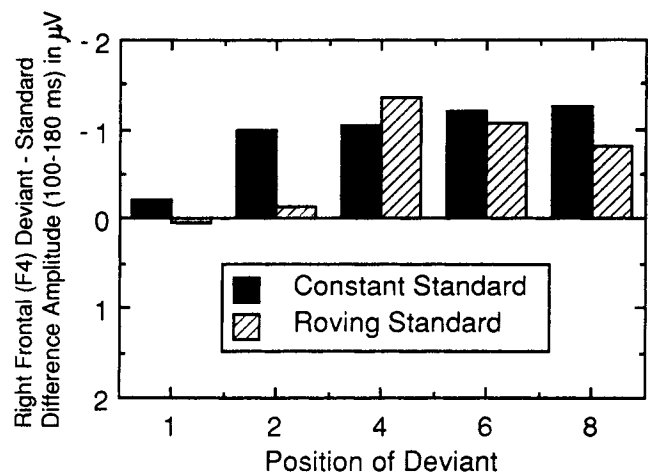
Figure 3. Across-subject-averaged mean mismatch negativity (MMN) amplitudes (average of the 100–180-ms interval), for each position at which a deviant could occur. Solid bars indicate the constant-standard condition, and striped bars indicate the roving-standard condition. (Negative values appear above baseline, and positive values appear below.)
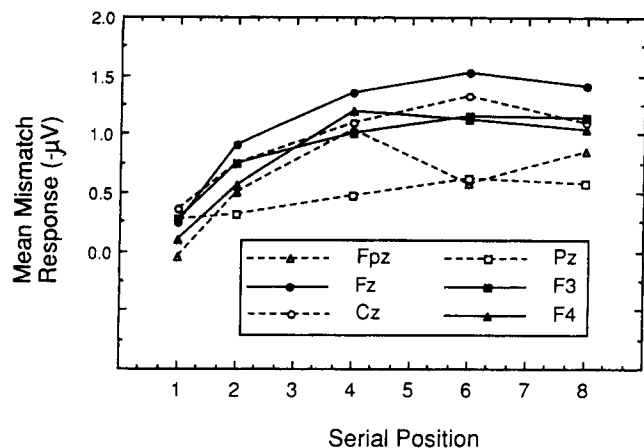
Figure 4. Mean mismatch (deviant – standard) response magnitudes across conditions for each serial position (*x* axis) and electrode (see inset legend).

Position 1 scores were significantly less negative than each of the other four positions at which deviants could occur, at $p < .05$ or better. The comparable analysis for the roving-standard condition also yielded a significant effect of position, $F(4, 44) = 4.17, p < .02, MS_e = 1.02$. However, in this condition the post hoc comparisons indicated only that Positions 1 and 2 both were significantly less negative than Position 4. (With t tests, Positions 1 and 2 both would be significantly less negative than Positions 6 and 8, as well.)

At Electrode F4, even the signs of the mismatch responses in the two conditions were markedly different in Position 2. In the constant-standard condition, all 12 individual subject means were negative at Position 2 (vs. 6 subject means at Position 1), whereas in the roving-standard condition, only 5 individual subject means were negative at Position 2 (again vs. 6 subject means at Position 1).

Stable Individual Differences in the Magnitude of the MMN

Because subjects differed in the magnitude of their MMN responses, we set out to determine the extent to which these differences represent personal traits versus session-specific states. This question was investigated by correlating subjects' mean scores in the constant-standard condition and the roving-standard condition, separately at each position. There was a significant correlation at Position 4, $r = .67, p < .02$. Although none of the other correlations reached significance ($rs = -.32, -.07, .09,$ and $.37$ in Positions 1, 2, 6, and 8, respectively), the significant correlation appears to indicate that there are stable individual differences in the MMN.

The absence of correlations in Positions 1, 2, 6, and 8 might be expected on the basis of results previously described. The range of scores available for a correlation was restricted because of an absence of an MMN for both conditions in Position 1 and for the roving-standard condition in Position 2. In Positions 6 and 8, the MMN was asymptotically stable in both conditions, again restricting the range of scores. Figure

4 shows that the MMN was not yet asymptotically large by Position 4, thus providing the variability needed for a correlation to be observed.

N1 Responses

We have noted that the MMN response is part of a more complex sequence of neural responses to a stimulus. New stimulus elements elicit an increased N1 response and then, beginning somewhat later in the ERP, any discriminable change of stimulus attributes (thus, presumably a change in the neural model of the stimulus) elicits an MMN. Investigators have disagreed about whether to consider the N1 enhancement response to be a part of memory (cf. Näätänen, 1990; Picton, 1992; Williamson, Lü, & Kaufman, 1992). As one type of evidence bearing on this issue, we examined N1 responses to standards in the constant-standard condition and the roving-standard condition. A difference between conditions would suggest that the N1, like the MMN, is responsive to information presented over 11 s ago, and this would tend to favor the suggestion that the N1 response is an integral part of memory.

To examine N1 responses, an analysis of ERPs to standards following homogeneous sequences of standards was carried out, using the 80–120-ms interval (see Näätänen & Picton, 1987). This analysis was limited to Positions 1–6 because there were too few trials to obtain stable averages for Positions 7–9. The purpose of the analysis was to examine whether some stimulus-specific refractoriness can still affect the N1 amplitude after delays of 11–15 s. Unless stimulus-specific subcomponents of N1 have not yet fully recovered after delays of 11–15 s, N1 should not differ between the two conditions.

The means corresponding to this ANOVA are shown in Table 2, and a distribution of the responses across frontal and central electrode locations is depicted in Figure 5. A difference between conditions is suggested. Specifically, N1 was larger in the roving-standard condition for the first few positions only, which suggests that some of the habituation to the standard survived the intersequence delay of 11–15 s in

Table 2

Across-Subject-Averaged Mean N1 Amplitude (in Microvolts) to Standards Presented in Positions 1–6 in Each Condition

Position	Type of standard	
	Constant	Roving
1	−5.549	−6.579
2	−3.166	−3.590
3	−2.192	−2.383
4	−2.501	−2.554
5	−2.348	−2.785
6	−2.801	−2.677

Note. N1 amplitude was measured as the average amplitude in the 80–120-ms interval of the event-related potentials to standard stimuli following homogeneous sequences of standards.
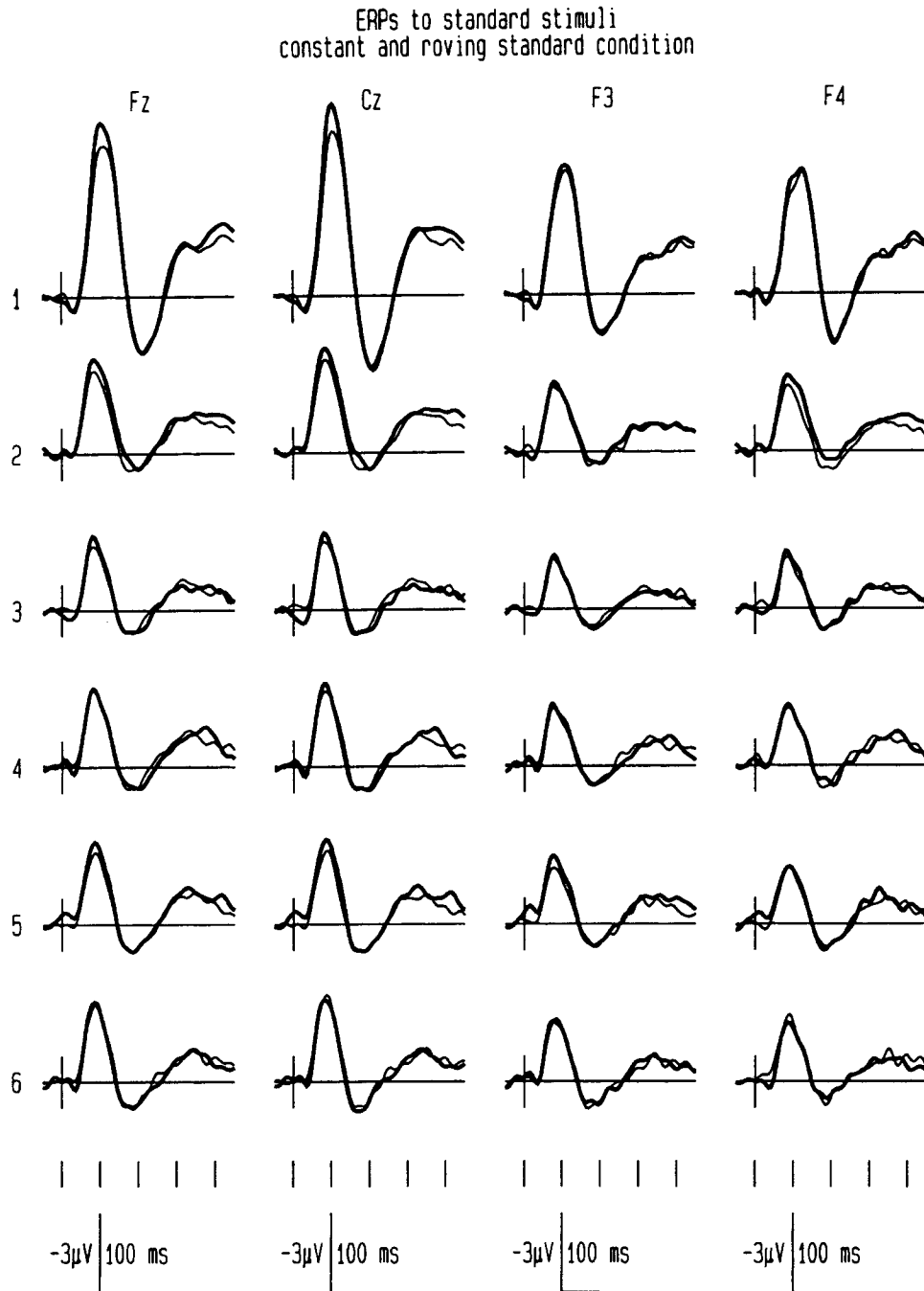
ERPs to standard stimuli
constant and roving standard condition

Figure 5. Across-subject-averaged event-related potentials (ERPs) to standard stimuli following homogeneous sequences of standards at Positions 1–6 (rows) for locations midline frontal (Fz; first column), midline central (Cz; second column), left frontal (F3; third column), and right frontal (F4; fourth column). The thick line indicates the roving-standard condition, and the thin line indicates the constant-standard condition. (Negative values appear above baseline, and positive values appear below.)

the constant-standard condition. The mean N1s in the two conditions decreased markedly across positions and became more similar to one another across positions, thus reflecting a well-known decrease of N1 in short-stimulus trains (Ritter, Vaughan, & Costa, 1968). In a two-way ANOVA of mean

ERP amplitudes (80–120 ms) measured from Cz, over which N1 is expected to peak (see Näätänen & Picton, 1987), with Positions 1–6 and condition as within-subject factors, significant effects were obtained for position, $F(5, 55) = 25.18$, $p < .0001$, $MS_e = 1.93$, and condition, $F(1, 11) = 6.62$, p

$< .03$, $MS_e = 0.61$, as well as for the Position $\times$ Condition interaction, $F(5, 55) = 2.87$, $p < .05$, $MS_e = 0.34$.

Discussion

The MMN has been taken to reflect a process in which the neural representation of each auditory stimulus is automatically compared with a neural model of the preceding stimuli and found to differ from it (Näätänen, 1990). This concept of a neural model is theoretically related to the concepts of neural (e.g., Hebb, 1949) and mental (e.g., Paivio, 1986) representation that have been important within experimental psychology. The MMN provides a clear neural index of this concept, but an empirical bridge between domains is needed.

A strategy for relating the MMN to other domains of learning and memory is to examine effects of similar manipulations across domains. One similarity is that there must be multiple presentations of a standard sound before an MMN to a deviant sound is elicited (Sams et al., 1984), which is similar to the finding that (a) multiple presentations of a stimulus result in habituation of the orienting response and the possibility for renewed orienting following a stimulus change (Sokolov, 1963), or (b) multiple presentations of a stimulus result in adaptation to the features present in that stimulus, with consequent perceptual aftereffects (e.g., see Goldstein, 1989). In each case, it can be assumed that some sort of memory representation that preserves information about the repeated stimulus is constructed through the repetitions. Also, in each case, the effect of repetitions decreases if time is allowed to pass following the last repetition. The representation fades or slips into a state that must be considered dormant, unused, or no longer contextually relevant. Finally, in many cases a memory representation that has become dormant can be reinstated or reactivated by a reminder presentation of the original stimulus or an associated stimulus (Rovee-Collier & Hayne, 1987; see Tulving & Thomson, 1973, for an elaboration of similar concepts in the case of explicit, conscious recall). The present study demonstrated this process of memory formation, inactivation, and reactivation in the case of simple tonal stimuli in an ignored channel leading to the MMN response within ERP recordings.

In the roving-standard condition of the present study, an MMN was obtained to a deviant tone after three or more presentations of the standard within the train, but not after only zero or one presentation. Presumably, then, the representation of the standard tone was built up during the first few repetitions of the standard within each tone train. In contrast, in the constant-standard condition, no MMN was obtained when the deviant tone occurred in Position 1. This finding is as expected if the memory representation becomes inactive or dormant during the 11–15-s silent delay between tone trains, which is in keeping with other studies indicating that the MMN does not occur with an intertone interval as long as this (e.g., Mäntysalo, & Näätänen, 1987). On the other hand, an MMN did occur at Position 2 and thereafter, following at least one presentation of the standard within the current tone train. Presumably, even a single presentation of the standard was sufficient to reactivate the representation of the standard tone.

On the basis of the present data, we cannot tell whether the origin of the prior memory representation in the constant-standard condition was local (i.e., was based on the immediately prior tone sequence) or global (i.e., was based on all prior sequences in combination). The results do, however, provide important information about the content of the memory representation. Research on musical cognition generally has focused on the finding that memory for relational information in a tone series is much better than memory for absolute pitch information (e.g., Dowling & Harwood, 1986). In accordance with such a view, absolute pitch information still would have to be present in sensory memory, but one might suppose that each tone's pitch would be retained only long enough to allow perception of the relational structure of a tone sequence, which would be saved much longer. However, the advantage of the constant-standard condition over the roving-standard condition in the present study indicates that the absolute pitch information itself must be held at least 11–15 s in memory. Moreover, the absence of a Position 1 MMN even in the constant-standard condition, and the potency of a single reminder presentation of the standard, suggest that this memory becomes dormant or inactive during the intertrain interval.

A memory that can become dormant and then reactivated might well be classified as a long-term memory, although we have not tested it over a long period. This is not an impractical suggestion, given that there have been other studies indicating that auditory memory of sensory qualities across much longer periods may exist (for a review see Cowan, 1984), such as memory for the voice of an acquaintance. Long-term sensory memory presumably would be less accurate than sensory memory of a very recent event, but that presumably still would be adequate for the present situation in which the difference between the standard and deviant tones was 17%, well over a semitone category (see Goldstein, 1989, p. 388).

In addition to the main result of the experiment, a process of habituation of the response to the standard tone across serial positions was observed. This habituation may index the creation of an active memory representation of the standard. Thus, Näätänen (1990) suggested that habituation of the N1 response is an indication that a neural model or representation has formed.

The present results are related to a debate on the nature of sensory memory. Näätänen (1990) implied that the memory of the standard that contributed to the MMN was a biologically determined memory. However, Port (1991) suggested that it might be a memory built up through experience. A finding of Näätänen (1991) and Schröger et al. (1992) that complex, multitone stimuli must be learned through repeated exposure before an MMN to a change can be obtained and the present finding on the value of a reminder presentation of a standard both support the view offered by Port. Sensory memory as observed in MMN studies apparently is not a separate memory faculty but rather a set of features, at least partly learned, that can be in a temporarily active state (cf. Cowan, 1988).

It seems remarkable to realize that learning in the present study took place in situations in which very little if any of

the subject's attention would have been directed toward the stimuli being learned. There are other recent studies, using behavioral rather than physiological measures, that also indicate that some types of learning can take place without focused attention or awareness (Jacoby, Woloshyn, & Kelly, 1989; Merikle & Reingold, 1991). In accordance with such sources of evidence, it is only the conscious, explicit knowledge of events that requires focused attention.

In addition to demonstrating that perceptual learning facilitates the MMN even for very simple stimuli, the ability of a single-tone presentation to reactivate a memory representation in the present study shows that a common phenomenon of learning, termed *single-trial reactivation* in the learning literature and *priming* in the more recent, cognitive literature (e.g., see Bower & Hilgard, 1981), contributes to the mismatch process. A single presentation of the standard tone was capable of priming, or reactivating, an already established memory of the standard, thus permitting an MMN to be elicited by the following deviant stimulus in the constant-standard condition.

This research leaves unsettled the basic form the representation of a simple tone would take. Why are repetitive presentations needed? There are several possibilities. The first is that the memory of an unattended tone is quite underspecified (cf. Cowan et al., 1990) and becomes more specific with repeated presentation. Thus, according to this view there should be an effect of the number of presentations on the smallest possible tone frequency change that would be discriminable or would elicit an MMN. Moreover, the delay period between tone trains would gradually degrade the specificity of the representation over time. The first postdelay presentation of the standard would increase the level of specificity quickly, much more quickly than if it were the very first presentation of the tone. This account assumes that there is a representation that can be in an active or a passive state, which is related to the usual assumption that there is a distinction between some sort of longer term and some sort of shorter term memory store.

Given that the subject was engaged in reading while the comparison of tones was carried out, the short-term store involved would not be assumed to imply conscious awareness of the tones. Within the model of Baddeley (1986), for example, it could reflect transient memory storage by a subservient system apart from the central executive. Similarly, within the model of Cowan (1988), the short-term store could reflect activated memory outside of the focus of attention.

A second version of the activation–decay–reactivation account seems to be more likely to us because it does not stipulate that multiple presentations are needed just to sharpen the memory of a simple tone. The second version states instead that the critical memory representation that must be built up is not the representation of a tone itself, but the representation of the status of the tone as a norm or standard. The representation in this account presumably is the same one that would allow a repeated stimulus within a novel channel of stimuli to be ignored (see Cowan, 1988; Sokolov, 1963), which is consistent with the proposal that the MMN generator process tends to elicit attention to the stimulus causing this MMN (Näätänen, 1990). Across the 11–15-s

delay, the particular standard representation would continue to exist in memory but would become dormant until a reminder presentation was provided. This account would help to explain why it is possible to obtain an MMN from a series of alternating tones that suddenly do not continue to alternate (Nordby et al., 1988). The representation that would be built up in that case would be the representation of a two-tone series, not of the two tones separately.

So far, these accounts have required that there be separate shorter and longer term memory faculties. It also is possible to formulate accounts that are based on a single memory faculty with complex properties. For example, one such account would be a variation of the previous, standard-as-norm account. In this account, the 11–15-s delay between tone trains would act by distancing the deviant from the train of standards and therefore placing it out of context. This is similar to the distinctiveness theories that have been offered to account for recency effects (Crowder, 1993; Neath & Crowder, 1990) and for both short-term and long-term modality effects (Glenberg, 1987) in list-recall studies. One problem with this account, however, is that it is based on relative rather than absolute quantities of time. Given that evenly spaced tones that are separated by several seconds or less consistently produce the MMN, tones evenly spaced but separated by longer intervals also should produce an MMN, but they do not appear to do so (Mäntysalo & Näätänen, 1987), although a response that may be an MMN recently was obtained by Böttcher-Gandor and Ullsperger (1992) using random intervals varying up to 10 s. If the durations of the tones were increased in proportion to the longer intertone intervals and an MMN clearly was obtained, then the contextual theory of the MMN could be vindicated.

As these considerations illustrate, it is going to be difficult to distinguish between the memory decay and distinctiveness–context type theories of forgetting and the reinstatement of memory. (As another example of this, Neill and Valdes, 1992, offered both types of theory as possible accounts of the time-dependence of negative priming phenomena.) However, a consideration of physiological as well as behavioral data soon may help to distinguish among theories. Proponents of distinctiveness accounts (Crowder, 1993; Glenberg, 1987) have used primarily behavioral evidence. No alternative distinctiveness account has been offered for physiological data that reveal a decrease in an observable neural response over time and that at least appear to require a decay account (e.g., Lü, Williamson, & Kaufman, 1992).

Also unsettled is the basis for individual differences in the MMN. We observed a correlation between conditions indicating that there are stable individual differences in MMN, but it is not clear if these individual differences would be consistent across stimulus types (e.g., across both tones and speech sounds).

In summary, the MMN is a useful physiological index of memory and a memory comparison process. The present evidence suggests that the concepts of memory representation, decay or inactivity of the representation, and reinstatement or reactivation of the memory are useful in this area, as they are in the field of cognitive psychology, despite the use of

simple tonal stimuli. We have pointed out areas in which future work may be usefully directed to allow a true convergence of behavioral and physiological methodology in the study of memory.

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