Central Auditory System Plasticity Associated with Speech Discrimination Training

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Abstract

■ A passively elicited cortical potential that reflects the brain's discrimination of small acoustic contrasts was measured in response to two slightly different speech stimuli in adult human subjects. Behavioral training in the discrimination of those speech stimuli resulted in a significant change in the duration and magnitude of the cortical potential. The results demonstrate that listening training can change the neurophysiologic responses of the central auditory system to just-perceptible differences in speech. ■

INTRODUCTION

Plasticity is an intrinsic characteristic of the central nervous system. It is well documented that neurophysiologic changes occur with experience or following trauma. Neural plasticity in the auditory system is most apparent in young animals during normal development (Rubel, 1978) or where sensory deprivation results in changes in the organization and function of auditory cortical neurons (Reale, Brugge, & Chan, 1987; Harrison, Stanton, Ibrahim, Nagasawa, & Mount, 1993). Changes in auditory cortex also occur in older animals after damage to peripheral sensory or neural structures (Robertson & Irvine, 1989; Pons, Garraghty, Ommaya, Kaas, Taub, & Mishkin, 1991). In humans, experience-related changes in central nervous system function have been demonstrated in individuals with peripheral hearing impairment (Neville, Schmidt, & Kutas, 1983; Gatehouse, 1992; Miyamoto, Osberger, Todd, Robbins, Karasek, Dettman, Justice, & Johnson, 1993).

Experience-related changes in adult auditory, somatosensory, and motor cortex appear when a behavior is elicited for a few minutes each day over a period of days or weeks (Merzenich, Grajski, Jenkins, Recanzone, & Peterson, 1991). Specifically, auditory cortex function is altered by training (Buchwald, Halas, & Schramm, 1966; Halas, Beardsley, & Sandie, 1970; Olds, Disterhoft, Segal, Kornblith, & Hirsh, 1972; Oleson, Ashe, & Weinberger, 1975; Recanzone, Schreiner, & Merzenich, 1993) and single auditory cortex neurons have been observed to change their firing patterns during the course of learning a new behavior (Kraus & Disterhoft, 1982; Weinberger, Hopkins, & Diamond, 1984).

In our research, we are interested in speech perception and its underlying neurophysiology. Understanding speech requires precise encoding in the peripheral auditory system and experience-dependent refinement of that encoding in the central auditory system. Of particular interest to us is whether central processing can be altered through training and whether rehabilitative efforts can improve the speech-processing capacity of the central auditory system in people whose nervous systems are underdeveloped or damaged.

Because speech is a complex and dynamic acoustic signal, central processing must be an inherently adaptive or plastic process that is especially sensitive to acoustic changes. The mismatch negativity (MMN) evoked potential is an auditory cortical response to acoustic change that is introduced in a repetitive stimulus sequence (Näätänen, Gaillard, & Mäntysalo, 1978; Näätänen & Picton, 1987; Csépe, Pantev, Hoke, Hampson, & Ross, 1993; Scherg & Picton, 1990; Giard, Perrin, Pernier, & Bouchet, 1990). The MMN is present even when the change is barely perceived behaviorally (Sams, Paavilainen, Alho, & Näätänen, 1985; Kraus, McGee, Micco, Carrell, Sharma, & Nicol, 1993a; Sharma, Kraus, McGee, Carrell, & Nicol, 1993) and shows plasticity in response to tonal stimuli (Näätänen, 1992).

Our goal was to determine whether training in speech-contrast discrimination would result in changes in the neurophysiology of the central auditory system. Because the MMN can reflect the central processing of fine stimulus differences, it shows promise as a tool for studying the neurophysiology underlying the perception of subtle speech contrasts. Consequently, we used the
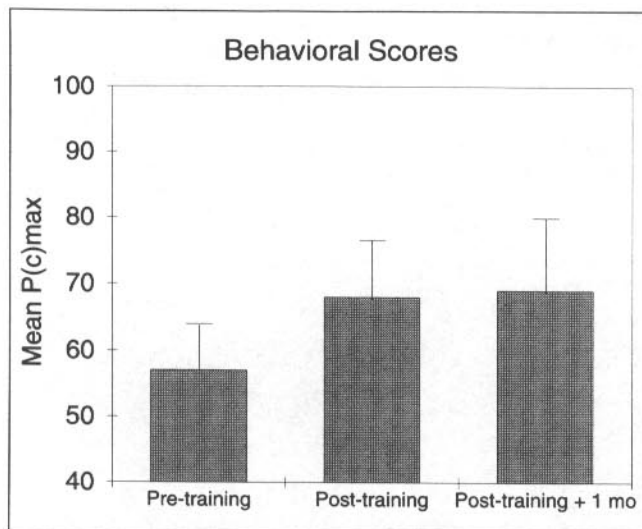
Figure 1. Behavioral discrimination [mean $P(c)_{max}$ scores] is shown pretraining, immediately post-training, and 1 month following the last training session. There was a significant improvement in pre- vs. post-training discrimination scores ($p < 0.05$). No significant change was evident immediately posttraining vs. 1 month later.
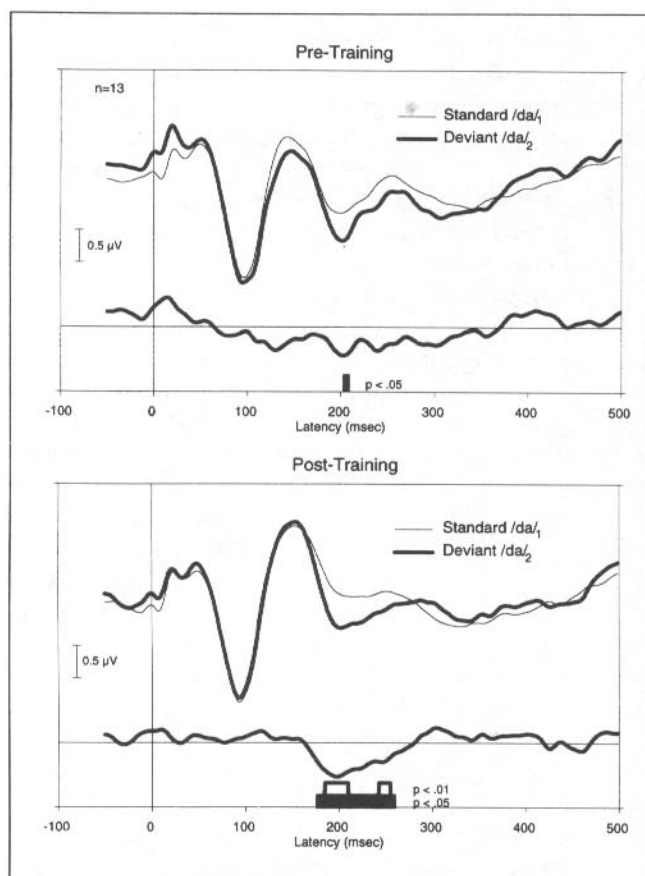

Figure 2. Mismatch condition. Grand average responses to standard and deviant stimuli pretraining (top) and post-training (bottom). Significant differences between the responses to standard and deviant stimuli are indicated by the box under the difference wave. The region of significance was larger post-training.

MMN to determine if changes in central auditory neurophysiology occurred as a result of listening training. If characteristics of the MMN were to change following speech-perception training or experience, then the possibility would exist for assessing the cortical neurophysiologic changes associated with auditory training, and for objectively evaluating the efficacy of auditory rehabilitation strategies.

RESULTS

Behavioral Discrimination

Behavioral results indicated a significant improvement in pre- vs. post-training discrimination of the two speech stimuli [$t(12) = 2.41, p < 0.05$]. The mean $P(c)_{max}$ scores were 56 and 67% before and after training, respectively. A $P(c)_{max}$ score of 50% indicates discrimination at chance level. Of the 13 subjects, six (46%) performed above chance by the sixth session ($p < 0.05$). Those results indicate that, although the discrimination was difficult, it could be learned.

The stability of the behavioral training was assessed one month following the last training session. Behavioral performance was remarkably stable. The average $P(c)_{max}$ score was 68% for the follow-up session and was not significantly different from the post-training data [$t(10) = 0.75, p > 0.05$]. Behavioral data are shown in Figure 1.

Electrophysiology

The MMN was present before training in 10 of the 13 subjects. After training, the MMN was present in all subjects. Figure 2 shows the grand average responses to the standard stimulus (/da/$_1$), the deviant stimulus (/da/$_2$), and the difference wave. The MMN is evident in the response to the deviant stimulus and is seen in the 200 msec region in the difference waveform. The N1 wave also is evident at about 100 msec in the response to both standard and deviant stimuli. The bar below the difference wave indicates the range over which the difference significantly differs from zero.

Figure 3 shows the grand average response to the /da/$_2$ stimulus when it was presented alone and when it was the deviant stimulus in the mismatch condition (see Methods for description of alone condition). The MMN is evident only in the second condition. The difference wave computed by subtraction of these waveforms results in a negativity in a latency region similar to the MMN in Figure 2. This negativity became larger after training.

Pre- and post-training MMN latency and magnitude values are detailed in Table I. MMN duration and area changed significantly with training. Overall duration changes reflect the changes in MMN onset and offset that occurred significantly earlier and later, respectively, with training. There was no significant change in peak latency of the MMN after training. Both onset-to-peak
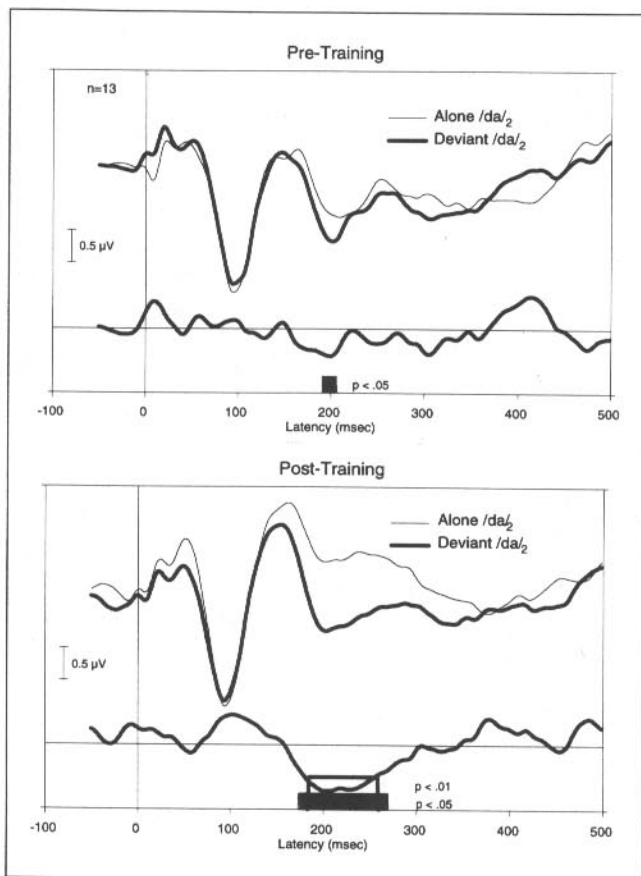
Figure 3. Alone condition. Grand average responses to the stimulus /da/₂ when it was presented alone (thin line) and when it was the deviant stimulus in the mismatch paradigm (thick line). The MMN occurs only in response to the /da/₂ stimulus in the mismatch condition. The difference between the response to /da/₂ in the two conditions was larger post-training compared to pretraining.

and peak-to-offset amplitudes were larger post-training, but only the onset-to-peak difference was significant.

Individual-subject changes in MMN duration are shown in Figure 4. Post-training changes are plotted relative to a normalized pretraining duration. No change is indicated by the zero line. A considerable increase in MMN duration was exhibited by 12 of the 13 subjects. The filled squares represent the duration change for those subjects who had an MMN in both pre- and post-training sessions. The open squares represent the data from the three subjects who had no MMN before training. Significant changes in duration occurred across subjects whether or not these three subjects were included in the data set. These changes were evident in both the mismatch (top) and "alone" conditions (bottom).

Individual pre- and post-training changes in MMN area are shown in Figure 5. A considerable increase in MMN area was exhibited by 11 of the 13 subjects. A significant increase in MMN area is evident in both the mismatch paradigm and in the "alone" condition.

DISCUSSION

This study showed that experience with a speech discrimination task results in a demonstrable neurophysiologic change in the MMN event-related potential. The change in the MMN is evidenced as an increase in response duration and magnitude. These findings are important for several reasons.

Underlying Neurophysiologic Mechanisms

Our findings are consistent with the observation that training induces increased temporal coherence in cortical neuron activity (Recanzone, Merzenich, & Schreiner, 1992; Recanzone & Merzenich, 1991). An increase in the number of neurons firing at or near the same time would result in an earlier and larger evoked response. By definition, evoked potentials are the product of multiple neuron activity. Therefore, these findings also support the notion that training results in the formation of "cell assemblies" that are increasingly synaptically linked to respond to conditioned stimuli (Merzenich et al., 1991).

These results further the understanding about the origins of the MMN response. The auditory thalamocortical pathways are thought to generate the MMN (Javitt, D., Schroeder, C., Steinschneider, M., Arezzo, J., & Vaughan, Jr., H., 1992; Javitt, 1992; Hari, Hämäläinen, Ilmoniemi, Kaukoranta, Reinikainen, Salminen, Alho, Näätänen, & Sams, 1984; Csépe, Karmos, & Molnár, 1987; Csépe, et al., 1992; Näätänen & Picton, 1987; Scherg & Picton 1990; Giard et al., 1990). Specifically, the nonprimary auditory pathway has been shown to contribute to the response (Kraus et al., 1994a,b). Learning-associated changes in single neuron activity are known to occur particularly in nonprimary subdivisions of the auditory cortex and thalamus (Kraus & Disterhoft, 1982; Weinberger et al., 1984). Thus it follows that evoked potentials demonstrating plasticity, and by inference the MMN, would receive contributions from non-primary areas central to the brainstem.

Relation between Behavioral and Electrophysiologic Changes

Learning-associated plasticity typically has been demonstrated in subjects actively performing a task associated with the experimental stimuli (Merzenich et al., 1991). The results of the current study suggest that active training associated with a particular stimulus can be reflected passively in the auditory system's response to the same stimulus even when the subject is not responding behaviorally to that stimulus or is attending to another unrelated task.

Behavioral discrimination ability can be reflected by the MMN (Sams et al., 1985; Lang, Nyrke, Ek, Aaltonen, Raimo, & Näätänen, 1989; Kraus, McGee, Ferre, Hoeppner, Carrell, Sharma, & Nicol, 1993c). The present

Table 1. Pre- vs. Post-training Comparison of MMN Latency and Magnitude in the Mismatch Condition and in the Alone Condition

	Pretraining (avg)	Post-training (avg)	t
Mismatch condition			
Latency (n=10)			
Onset (msec)	168	143	3.17*
Peak (msec)	220	219	0.13
Offset (msec)	278	315	2.51*
Duration (msec)	110	172	4.79***
Magnitude (n=13)			
Onset/Peak amplitude (μV)	1.1	1.4	2.26*
Peak amplitude/offset (μV)	1.2	1.6	1.51
Area (μV × msec)	98	150	3.18**
Alone condition			
Latency (n=10)			
Onset (msec)	164	160	0.28
Peak (msec)	220	229	0.39
Offset (msec)	270	321	2.58*
Duration (msec)	106	161	3.98**
Magnitude (n=13)			
Onset/Peak amplitude (μV)	1.1	1.8	4.52***
Peak amplitude/offset (μV)	1.3	2.3	5.47***
Area (μV × msec)	82	231	6.34***

*p < 0.05.
** p < 0.01.
***p < 0.001.

study is consistent with these earlier findings in that changes in behavioral discrimination were also reflected by changes in the MMN in the group data. Interestingly, post-training enhancement of the MMN remained stable in most subjects even though behavioral discrimination scores had not improved for some of them. As a pre-attentive response, the MMN may be showing a neurophysiologic improvement in discrimination that has not yet been integrated into a voluntary response. What is not known is whether these subjects would exhibit significant behavioral discrimination improvement with extended training.

Repetitive Stimulus Exposure and Attentional Effects

Post-training differences in the MMN appear to result solely from neurophysiologic changes associated with training. The modified MMN responses do not result simply from exposure to the stimuli. Studies have indicated that, in the absence of training, similar passively elicited evoked potentials are stable from session-to-session (Chertoff, Goldstein, & Mease, 1988). Specifically, the MMN is stable with a trend toward amplitude *decrement* (rather than enhancement) over time (Näätänen & Gaillard, 1983; Paavilainen, Cammann, Alho, Reinikainen, Sams, & Näätänen, 1987).

Post-training changes in the MMN also are not related to changes in attention to the stimuli. The behavioral discrimination data indicate that the stimuli remained difficult to discriminate in the quiet context of the behavioral experiment even after training. It is unlikely that the subjects could have detected the difference between the stimuli during the electrophysiologic recording when their attention was focused on an interesting movie and they also were listening to the soundtrack of the videotape in the nontest ear (Bregman & Campbell, 1971).

Summary

Training in the discrimination of just-perceptible differences in speech sounds resulted in changes in the duration and magnitude of the MMN, a passively elicited cortical potential. The results suggest that the MMN may serve as an objective indicator of neurophysiologic changes in the central auditory system resulting from learning or auditory experience. An objective tool for assessing auditory processing over time would be useful clinically in a variety of populations (e.g., young children with cochlear implants, school-age children with auditory processing disorders, the elderly, individuals with hearing aids). Therefore, the MMN may be a tool for the measurement of neurophysiologic changes that accompany speech listening training, and for the objective
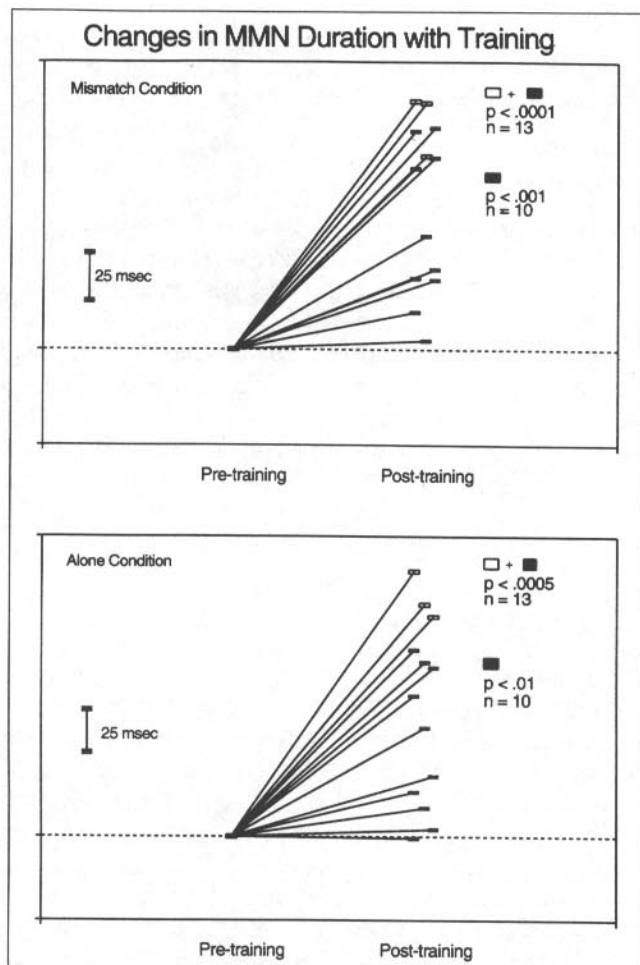
Figure 4. Individual-subject changes in MMN duration after training in the mismatch (top) and alone (bottom) conditions. Post-training changes are plotted relative to normalized pretraining durations. No change is indicated by the zero (dotted) line. The filled squares represent the duration change for those subjects who had an MMN both in the pre- and post-training sessions. The open squares represent the data from the three subjects who had no MMN before training. Significant changes in duration occurred irrespective of whether these three subjects were included in the data set.

evaluation of the efficacy of auditory rehabilitation strategies, hearing aids, and cochlear implants.

METHODS

Thirteen healthy normal-hearing adult subjects were trained to discriminate between two similar-sounding synthetic speech stimuli. The stimuli were variants of the phoneme /da/ that were produced using a Klatt (1980) digital speech synthesizer. Acoustically, the two stimuli differed in the onset frequencies of the second and third formant transitions. These stimuli have been described in more detail elsewhere (Kraus, et al., 1993a; Kraus, Micco, Koch, McGee, Carrell, Wiet, Weingarten, & Sharma, 1993b), and are referred to as $/da/_1$ and $/da/_2$. In an
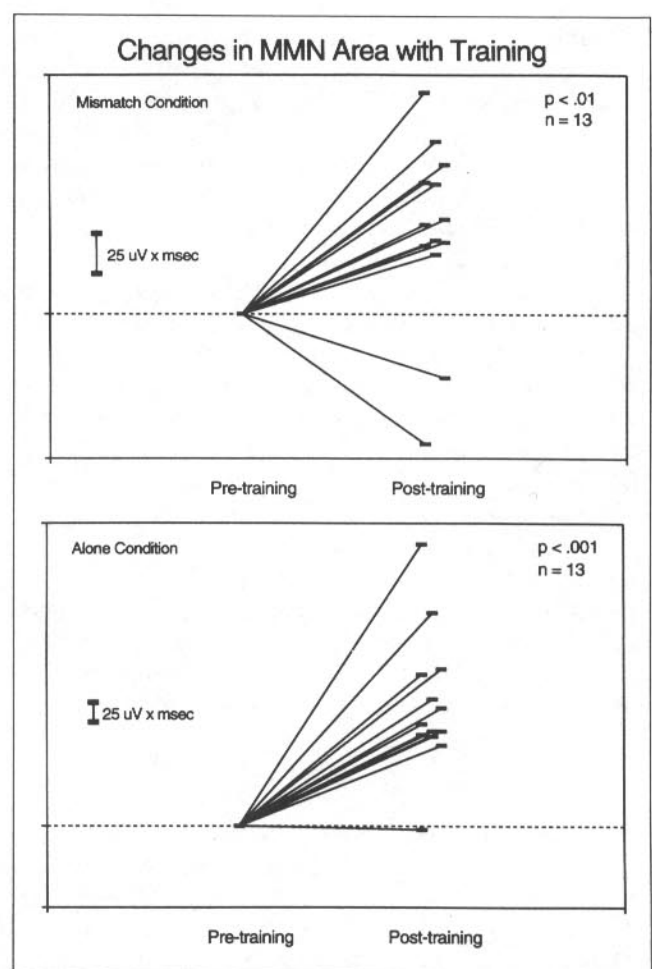

Figure 5. Individual-subject changes in MMN area after training in the mismatch (top) and alone (bottom) conditions. Post-training changes are plotted relative to normalized pretraining areas. No change is indicated by the zero (dotted) line. Significant increases in MMN area are evident with training.

earlier identification experiment (Sharma et al., 1993), $/da/_1$ was perceived as /da/ 100% of the time and $/da/_2$ was perceived as /da/ 96% of the time.

The training paradigm consisted of a same–different two-alternative forced-choice discrimination task. Visual feedback was presented after each trial to indicate whether the preceding response was correct. An identification paradigm with similar feedback and timing has been shown to be effective in training subjects to discriminate difficult speech contrasts (McClasky, Pisoni, & Carrell, 1983). Previous studies have shown that minimal stimulus uncertainty and short interstimulus intervals along with rapid visual feedback facilitate training (Pisoni, 1973; Carney et al., 1977; Werker & Logan, 1985). This methodology allowed listeners to direct their attention to the contrast being trained and to base their responses on echoic memory. Longer interstimulus intervals and more complex paradigms, on the other hand,

forced subjects to base their responses on more categorized or phonetic representations in memory (Logan, Lively, & Pisoni, 1991). Because we were interested in utilizing a training procedure that is likely to engage the earliest stages of processing of speech signals, we used a short inter-stimulus interval and minimal stimulus uncertainty procedure with feedback for training and behavioral testing.

Over the course of 1 week, subjects underwent six 1-hr discrimination training sessions. Stimulus pairs (interstimulus interval = 1 sec) were presented in blocks of 54 with four blocks per session. The subject had 3 sec to respond by pressing a button labeled "same" or "different." A feedback light indicated whether the response was correct or incorrect. $P(c)_{max}$ was calculated for each trial block and averaged across each training session. $P(c)_{max}$ is a measure of behavioral discrimination that combines signal detection measures of d' and B to create an unbiased measure of discriminability (Green & Swets, 1974). To assess the stability of behavioral performance over time, 11 of the 13 subjects were retested 1 month or more following the last training session.

Mismatch Condition

MMN responses were recorded immediately before the first training session and immediately after the sixth session. The MMN was elicited by the same synthetic speech stimulus pair used for behavioral training. Speech stimuli were presented through insert earphones to the right ear at 75 dB SPL. Subjects were instructed to watch videotaped movies. The sound-field audio levels of the videotape were less than 40 dB SPL.

The stimuli were presented using an oddball paradigm in which the deviant stimulus $/da/_2$ (probability of occurrence = 15%) was presented in a series of standard stimuli $/da/_1$ (probability of occurrence = 85%). Stimuli were presented in a pseudorandom sequence (interstimulus interval = 1 sec) with at least three standard stimuli separating presentations of deviant stimuli.

Evoked responses were recorded from Fz/A2 with the forehead as ground. Eye movements were monitored with a bipolar electrode montage (supraorbital-to-lateral canthus). The recording window included a 50 msec prestimulus period and 500 msec of poststimulus time. Evoked responses were analog bandpass filtered on-line from 0.1 to 100 Hz (12 dB/octave). Responses were digitally low-pass filtered off-line at 40 Hz with a Blackman filter.

Evoked responses elicited by standard stimuli and by deviant stimuli were averaged separately. Responses were elicited in trial blocks of 25 deviant and approximately 140 standard stimuli. At least 10 such trial blocks were summed to produce a grand average for each individual. An equal number of trial blocks were used for each subject, before and after training. The individual grand averages consisted of responses to a minimum of 250 deviant and 1400 standard stimuli. A difference wave was calculated for each subject by subtracting the standard response from the deviant response.

Alone Condition

By definition, the MMN is a response to stimulus change. It occurs when the deviant stimulus $(/da/_2)$ is presented in the context of standard stimuli. The evoked response to the deviant stimulus presented alone should not elicit a mismatch response. Therefore, responses to the $/da/_2$ stimulus presented alone were compared to the responses to the same $/da/_2$ stimulus presented in the mismatch condition. These stimuli were also presented with an interstimulus interval of 1 sec. Individual grand averages consisted of responses to 250 stimulus presentations.

Data Analysis

Pre- and post-training grand averages were computed across subjects as previously described (Kraus et al., 1993a,b). A point-by-point t test of the values of the contributing waveforms determined the latency duration over which the responses to standard and deviant stimuli were significantly different. The MMN was considered to be present if a significant difference (negativity) occurred between 150 and 350 msec in 60th mismatch and alone conditions. MMN amplitude, latency, duration, and area were measured from the individual grand average difference waves. MMN peak latency was measured between 150 and 350 msec. Duration was defined as the offset minus the onset latency. MMN magnitude was computed by measuring (1) the amplitude from the preceding peak to the midpoint of the MMN (onset-to-peak) and from the midpoint to the end of the MMN waveform (peak-to-offset) and (2) the area of the MMN waveform. To measure the area, a line was drawn between the onset and offset of the MMN in the difference wave, and the enclosed area of the difference waveform was measured resulting in a unit of msec $\times$ μV. Similar statistics were performed comparing the $/da/_2$-alone waveform with the $/da/_2$- deviant (mismatch) waveform.

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