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Evoked-potential changes following discrimination learning involving complex sounds

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Abstract

Objective—Perceptual sensitivities are malleable via learning, even in adults. We trained adults to discriminate complex sounds (periodic, frequency-modulated sweep trains) using two different training procedures, and used psychoacoustic tests and evoked potential measures (the N1-P2 complex) to assess changes in both perceptual and neural sensitivities.

Methods—Training took place either on a single day, or daily across eight days, and involved discrimination of pairs of stimuli using a single-interval, forced-choice task. In some participants, training started with dissimilar pairs that became progressively more similar across sessions, whereas in others training was constant, involving only one, highly similar, stimulus pair.

Results—Participants were better able to discriminate the complex sounds after training, particularly after progressive training, and the evoked potentials elicited by some of the sounds increased in amplitude following training. Significant amplitude changes were restricted to the P2 peak.

Conclusion—Our findings indicate that changes in perceptual sensitivities parallel enhanced neural processing.

Significance—These results are consistent with the proposal that changes in perceptual abilities arise from the brain's capacity to adaptively modify cortical representations of sensory stimuli, and that different training regimens can lead to differences in cortical sensitivities, even after relatively short periods of training.

Keywords

Plasticity; frequency-modulated sounds; spectrotemporal

Introduction

It is now widely accepted that perceptual sensitivities are not fixed throughout the lifespan. Rather, they can be altered by learning and experience, even in adult humans and non-human animals (Fahle and Poggio, 2002). Such perceptual adaptability is thought to reflect

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enhancement in the processing of sensory stimuli, allowing events that are behaviorally relevant to be processed more efficiently. The mechanisms underlying such changes are, however, not well understood.

Recent studies of learning-induced plasticity in humans have focused on evaluating neural changes following training by use of auditory evoked-potentials (AEPs). The N1-P2 complex is one of the long-latency AEPs shown to be modifiable through experience. The N1 response is characterized by a negative deflection peaking at about 100 ms post stimulus onset (ranging from 75 to 150 ms), with maximum amplitude recorded from frontocentral areas (Vaughan and Ritter, 1970) or the vertex (Picton et al., 1974). The subsequent P2 response is a positive peak with a latency of approximately 175 ms (ranging from 150 to 275 ms) (Wood and Wolpaw, 1982). These two peaks are thought to be independently generated, reflecting distinct neural processes (Knight et al., 1988; Tremblay and Kraus, 2002).

The N1-P2 complex can be elicited by various perceptible changes in the auditory environment. Such changes include the onset of transient sounds such as clicks, tones, speech sounds and noise bursts, as well as abrupt changes in stimulus features such as loudness, pitch, or perceived location of continuous sound (for a review, see Hyde, 1997). The amplitude of the N1-P2 complex has been shown to correspond closely to the intensity of the auditory stimulus, indicating that N1-P2 can be used as a non-behavioral estimate of individual sensitivity to acoustic parameters (i.e., physiological threshold estimation). N1-P2 amplitude has also been shown to reflect the magnitude of change in stimuli, indicating that this complex may be used to measure difference limens (Fowler and Mikami, 1992). The fact that the N1-P2 complex can be used as an objective, physiological measure of change detection suggests it could be a valuable tool for studying relationships between perceptual and neural sensitivities to various acoustic features (Alain et al., 2010; Ross and Tremblay, 2009; Tremblay et al., 2009; Tong et al., 2009).

In the present study, we aimed to better understand the neural mechanisms underlying auditory perceptual learning following discrimination of non-linguistic complex sounds. We trained participants in two experiments and manipulated the amount of training across experiments. Participants were trained to discriminate sounds with a high degree of acoustic similarity; their behavioral performance and electrophysiological responses were measured before and after training. The stimuli we used were periodic, frequency-modulated sounds with varying intrinsic temporal properties (e.g., sweep repetition rate). Several mammalian species use rapid frequency modulation to communicate significant information (Brown et al., 1978; Kaltwasser, 1990; Newman, 1978; Suga, 1968; Winter et al., 1996), and thus rely heavily on their capacity to represent such dynamic features of sounds. In humans, rapid changes in frequency content serve as one of the cues for discriminating consonant-vowel syllables (Fitch et al., 1997). We believe, therefore, that it is important to use sufficiently complex acoustic stimuli in order to obtain a more complete characterization of the neural processes underlying auditory training.

To further explore the factors impacting learning and plasticity, two training regimens were compared in both experiments. Participants were either trained exclusively with a pair of highly similar target sounds, or with less similar sounds that became progressively more similar as training progressed. Previous findings have indicated that learning of difficult discriminations can be facilitated by progressively requiring participants to detect finer perceptual differences (e.g., Tallal et al., 1996). Therefore, we expected to observe greater changes in both perceptual and neural sensitivities as a result of progressive training. A direct comparison of different training techniques allowed us to evaluate training-induced differences in the amount and efficiency of learning. The N1-P2 responses we recorded were

evoked by deviant complex sounds within a continuous sequence of standards (i.e., change detection responses).

A better understanding of the neural correlates underlying perceptual learning also has important practical relevance, because training-based therapeutic techniques have enormous potential for helping individuals with perceptual deficits to overcome their limitations (Tallal et al., 1993, 1996; Temple et al., 2003).

Experiment 1

Methods

Participants—Twenty-seven healthy adults (mean age = 22.35, range 19 – 30 years) from the University at Buffalo were recruited for this study through advertisements posted around the campus. All participants provided written informed consent and received monetary compensation for their participation. All had self-reported normal hearing. Nine participants were assigned to each of three groups (progressive training, constant training, or control).

Design—The sounds used for behavioral and electrophysiological testing were periodic upward-moving frequency sweeps (for details, see Supplementary Material: Methods). The experiment took five consecutive days to complete. Each participant was trained with one of the three stimulus regimens for one daily session. The day before and the day after training, participants received a behavioral test to assess their perceptual sensitivity to the sounds. The day before and the day after behavioral tests, participants were presented with the sounds and their auditory evoked potentials were recorded. Details of the training, behavioral and electrophysiological tests are described in the Supplementary Material: Methods.

Electrophysiological recordings—Electrophysiological recordings took place on days one and five of the experiment. Electroencephalogram (EEG) was recorded through Ag/AgCl electrodes. The electrodes were connected to a NuAmp amplifier (Neuroscan®) with an online filter of 0.1 to 100 Hz and recorded with a sampling rate of 1000 Hz. Signals were recorded from sixteen electrodes at the Fz, FCz, Cz, Pz, F3, F4, F8, C3, C4, T4, T5, T6, P3, P4, O1, and O2 sites (International 10–20 system) with the left mastoid as the reference and AFz as the ground. Two additional electrodes were placed above and below the left eye to monitor vertical ocular movements. Impedances of all electrodes were kept below 15 k Ω .

Participants were seated in an acoustically shielded room and were instructed to ignore the stimuli and to read material of their choosing. They were also instructed to advise the experimenter if they felt tired or drowsy, and were given multiple opportunities for breaks during the recording session. Each recording session lasted approximately 3 hrs. Sounds were delivered monaurally to the left ear using an Etymotic-Research (ER-3) insert earphone (an earphone was also positioned in the right ear although no sound was delivered through it). Sounds were presented using a presentation schedule in which three standard sounds were followed by one deviant sound, and recording was time-locked to the presentation of the deviant sound. The purpose of this schedule was to set a predictable point of potential auditory change. The stimuli used for electrophysiological testing were a subset of those used for behavioral testing and training. Each recording session comprised six different testing conditions differing in the deviant sound that was presented. For all conditions, we used a 12 Hz sound as the standard sound. The respective deviant sounds in the six testing conditions were 2, 4, 6, 8, 10, and 11 Hz. In addition, all participants were presented with a control condition in which the standard sound (12 Hz) was repeatedly presented and recordings were obtained at every fourth presentation. During testing, sound was presented continuously, with no silent interval between stimuli. Inter-stimulus intervals

ranging from 0–600 ms were tested in pilot studies and the most robust responses were observed under the condition of no inter-stimulus interval. Sound presentation and the delivery of event codes marking the onset of standard and constant sounds in the recording system were controlled by E-prime running on a different computer.

Results

Behavioral data—The mean discrimination accuracies by sweep repetition rate for the pretest and posttest in the progressive, constant, and control groups are listed in Table 1. Because we used a three-alternative, forced choice task for these tests, chance level performance was 33%. Given that each deviant sound was presented 40 times, accuracy rates higher than 48% (two-tailed, 46% for one-tailed) were significantly above chance. Unless otherwise noted, the α value of all statistical tests in the study is set at .05.

To determine whether participants in each group showed an overall improvement in discrimination from pretest to posttest, the mean accuracies across all tested repetition rates were entered into a 3 (group: progressive, constant, control) \times (2) (test: pretest, posttest) mixed analysis of variance (ANOVA). We found a significant group \times test interaction, $F(2, 24) = 7.70$, $p = .003$, $\eta_p^2 = 0.39$. None of the main effects were significant. Three additional planned comparisons between the mean pretest and posttest accuracies by group revealed that the overall performance accuracy improved from pretest to posttest in the progressive group, $t(8) = 3.53$, $p = .008$, but not in the constant and control groups. The mean percent correct in pretest and posttest by group is presented in Figure 1.

To compare the training effects in greater detail, we calculated the pretest to posttest difference in performance accuracy by each repetition rate. This measure is referred to hereafter as the difference score. Difference scores were entered into a 3 (group: progressive, constant, control) \times (15) (deviant repetition rate: 2, 4, 6, 8, 10, 11, 11.1, 11.2, 11.3, 11.4, 11.5, 11.6, 11.7, 11.8, 11.9 Hz) mixed ANOVA. This analysis revealed a significant main effect of group, $F(2, 24) = 7.70$, $p = .003$, $\eta_p^2 = 0.39$, as well as a main effect of rate, $F(14, 336) = 3.91$, $p = .000$, $\eta_p^2 = 0.14$. A trend for the group \times rate interaction was observed, $F(28, 336) = 1.45$, $p = .068$, $\eta_p^2 = 0.11$.

We further examined two particular planned contrasts of interests. The first was the difference score for the deviant repetition rate of 11.5 Hz among the three groups; the 11.5 Hz sound was what participants in the constant training group were asked to distinguish from a 12 Hz sound. Improvement discriminating the 11.5 Hz deviant from pretest to posttest was significantly greater in the progressive group in comparison to the constant and control groups, $t(16) = 4.00$ and 3.02 respectively, $ps < .01$. However, no difference was found between the constant and control groups. The second planned contrast involved comparing the mean difference scores among the three groups for the deviant repetition rates not experienced during training (including 11.1, 11.2, 11.3, 11.4, 11.6, 11.7, 11.8, and 11.9 Hz). This contrast examined the extent to which discrimination training generalized to stimuli not used during training. Sounds with a lower deviant repetition rate were excluded because discrimination accuracies were at ceiling prior to training. A similar pattern to the first contrast of interest was found: the mean difference score for the progressive group was significantly greater than for the constant and control groups, $t(16) = 2.88$ and 3.33 respectively, $ps \leq .01$. The constant and control groups were essentially the same. This indicates that participants trained in the progressive condition were better able to generalize training to untrained sounds in the posttest than those in the other two groups.

Electrophysiological data—The mean P2 amplitude averaged across all deviant repetition rates was entered into a 3 (group: progressive, constant, control) \times (2) (test: pretest, posttest) \times (16) (electrode) mixed ANOVA. A complete list of the results is

presented in Table 2. The group \times test interaction was marginally significant. All main effects and remaining two-way interactions were significant. In general, peak P2 amplitude was greater in the posttest than in the pretest. This difference was only statistically significant in the progressive group, $t(8) = 4.68, p = .002$. The mean P2 amplitudes in pretest and posttest as a function of training group are presented in Figure 2. Consistent with previous literature, the greatest P2 amplitudes were recorded at Cz in both pretest and posttest (see Figure 2).

To further examine the effect of training on P2 amplitude, P2 difference scores were entered into a 3 (group: progressive, constant, control) \times (7) (deviant repetition rate: 2, 4, 6, 8, 10, 11, 12 Hz) \times (16) (electrode) mixed ANOVA. The group main effect was marginally significant, $F(2, 24) = 3.24, p = .057, \eta_p^2 = 0.21$. Planned contrasts revealed that overall, P2 difference scores of the progressive group were greater than that of the constant group, $t(16) = 2.33, p = .033$, and marginally greater than that of the control group, $t(16) = 2.04, p = .058$. The main effects of deviant rate and electrode, as well as the rate \times electrode interaction were significant. A complete list of the results from this analysis is presented in Table 3. Overall, P2 difference scores diminished as the deviant sound became more similar to the standard sound, $F(6, 144) = 6.79, p = .000, \eta_p^2 = 0.22$. To examine the effect of deviant rate at each electrode, we conducted a custom contrast at each electrode in which the amplitude of P2 evoked by the 2, 4, and 6 Hz deviants was compared with that evoked by the 10, 11, and 12 Hz deviants. The results are shown in Table 4. The threshold for significance was .0031, using a joint significance level of .05 across the 16 contrasts. We found that the effect of deviant rate was consistent across all electrodes except for T5, T6, O1, and O2 (see also Supplementary Material: Results).

Experiment 2

Methods

Participants—Twenty-seven healthy adults (mean age = 23.9, range 18–36) from the University at Buffalo were recruited for this study through advertisements posted around the campus. All participants in the study provided written informed consent and received monetary compensation for their participation. All had auditory thresholds of ≤ 20 dB HL (ANSI, 1989) for octave frequencies from 250 to 8000 Hz in the tested/trained ear. Nine participants were assigned to each of the three groups (progressive, constant, or control).

Design—The sounds used in Experiment 2 were identical to those used in Experiment 1. The design of Experiment 2 was identical to Experiment 1 with the following exceptions. First, participants were trained in eight daily sessions instead of only one. Consequently, the experiment took 12 days to complete. Additionally, participants in the control condition received no training instead of being exposed to the progressive training sound while being trained on a visual task. Discrimination tests were conducted on days two and eleven of the experiment and took place in a sound attenuated booth. The task was identical to that used in Experiment 1, except that sounds were presented monaurally to the left ear through insert earphones, Etymotic research (ER-3), and participants responded using a button box rather than a keyboard. Feedback of a correct response was a lit solid light directly above the chosen button, whereas an incorrect response resulted in a blinking light above the button corresponding to the correct choice. Training took place in the sound attenuated booth, and consisted of eight discrimination sessions across eight consecutive days (days 3–10). The training task was identical to that in Experiment 1 for the constant group. For the progressive group, the slow sound remained constant within a training session, but became more similar to 12 Hz across training sessions (see Figure 3 for the progression). Participants in the control group did not receive any training and did not report to the lab during the eight days between tests.

Electrophysiological recordings—Electrophysiological recordings took place on days one and twelve of the experiment. Gold electrodes were attached to the scalp at the vertex location (Cz, active), left mastoid (reference) and forehead (ground). Thus electrical activity was recorded mainly from the left hemisphere. Electrophysiological activity was digitized and amplified using Tucker-Davis-Technologies (TDT) hardware and software system (Software was BioSig 32). Responses were recorded using a 500 ms window, filtered online with a cut-off frequency of 30 Hz, and amplified with a gain of 50 K. An analog to digital sampling period of 50 ms was used. Trials with artifacts exceeding 100 μ V were excluded from analyses. Averages included 100 trials, and two averages were collected per condition to ensure reliability. A PC (DOS)-based system controlled the timing of stimulus presentation and delivered an external trigger to the evoked potential system to record responses evoked by the deviant stimulus. The recording conditions were identical to those in Experiment 1.

Results

Behavioral data—The mean discrimination accuracies by deviant repetition rate for the pretest and posttest in the progressive, constant, and control groups are listed in Table 5. To determine whether participants in each of the conditions showed improved discrimination from pretest to posttest, the mean accuracy across all sweep repetition rates was entered into a 3 (group: progressive, constant, control) \times 2 (test: pretest, posttest) mixed analysis of variance (ANOVA). The results of this analysis revealed a significant effect of test, $F(1, 24) = 10.30, p = .004, \eta_p^2 = 0.30$. Although the group \times test interaction was only marginally significant, $F(2, 24) = 2.96, p = .071, \eta_p^2 = 0.20$, three planned contrasts were conducted to compare the mean pretest and posttest accuracies in each group. On average, trained participants performed better in the posttest than in the pretest: $t(8) = 2.64$ and $3.04, ps = .030$ and $.016$ for the progressive and constant groups, respectively. Untrained participants (control group) showed similar performance levels before and after training, $t(8) < 1$, indicating that exposure to the sounds during the discrimination pretest was not sufficient to induce better performance in the posttest. These results are shown in Figure 4.

To examine the training effects in greater detail, difference scores between pretest and posttest were calculated for performance accuracy at each sweep repetition rate for each participant. Before proceeding, we evaluated whether the degree of change in discrimination capacities (i.e., difference scores) correlated with participants' baseline abilities to distinguish the sounds (i.e., pretest performance)¹. For each group, a Pearson correlation was calculated within each group between the mean individual pretest accuracy and the difference score. The correlation coefficient was positive for both the progressive and constant groups, $r(7) = .49$ and $.60, p = .18$ and $.085$, respectively. In contrast, the coefficient was negative for the control group, $r(7) = -.12, p = .75$. Although none of these within-group correlations was statistically significant, the pooled coefficient between the progressive and constant groups showed a significant positive correlation for the trained participants, $r(16) = .50, p = .03$. This indicates that the degree to which a participant's test performance benefited from training was predicted by the sensitivity with which that participant distinguished sounds prior to training.

The difference scores were submitted to a 2 (group: progressive, constant) \times 15 (deviant repetition rate: 2, 4, 6, 8, 10, 11, 11.1 11.2, 11.3, 11.4, 11.5, 11.6, 11.7, 11.8, 11.9 Hz) mixed analysis of covariance (ANCOVA), with pretest accuracies of repetition rates of 10 Hz and above used as covariates in the analysis. ANCOVA was chosen to rule out the contribution

¹The same analysis was also conducted in Experiment 1, and the correlations between pretest accuracies and difference scores remained non-significant even after the trained groups were pooled to increase power.

of pretest accuracies to the difference scores. Pretest accuracies for 2 to 8 Hz sounds were excluded due to ceiling level performance at these deviant rates (see Table 5). The control group was excluded from this analysis because participants' performance levels did not improve, and no correlation was found between their pretest and difference scores.

This analysis revealed a significant group \times deviant rate interaction, $F(14, 70) = 4.61, p = .000, \eta_p^2 = 0.48$, and a marginally significant effect of group, $F(1, 5) = 4.81, p = .080, \eta_p^2 = 0.49$. The main effect of deviant rate was not significant. The significant interaction indicates that participants' sensitivity to various sound contrasts was differentially enhanced in the progressive and constant training groups. Further exploration with ANCOVAs on two subsets of the data revealed that participants in the progressive group exhibited greater improvement for the hardest (but still possible) sound contrasts (10 Hz and above) than participants in the constant group: $F(1, 5) = 7.09$ and $F(10, 50) = 4.46, p = .045$ and $.000, \eta_p^2 = 0.59$ and 0.47 for the main effect of group and the group \times deviant rate interaction, respectively. However, there were no significant effects for those sound contrasts that participants could discriminate well prior to any training (8 Hz and below).

Two additional planned contrasts were of interest. One compared the difference scores for each group at the deviant rate of 11.5 Hz - the target training contrast for both the progressive and constant groups, and the only contrast experienced by the constant group during training. The progressive group showed greater improvement than the constant group, $t(5) = 3.50, p = .017$ at distinguishing this rate from 12 Hz. To assess the degree of generalization of distinct training regimens, the second contrast involved difference scores at deviant rates that were not experienced by participants during training. We compared the group performance at the novel deviant rates of 11.1, 11.2, 11.4, 11.6, 11.7, 11.8, and 11.9 Hz (2, 4, and 6 Hz were excluded because of ceiling performance prior to training). This comparison also yielded a significant group difference, $t(5) = 2.64, p = .046$, indicating that the progressive group better generalized training to sounds with novel deviant repetition rates than did participants in the constant group.

Electrophysiological data—Figure 5 shows the grand-average waveforms time-locked to the onset of the deviant sounds at Cz as a function of group and deviant sound. The corresponding waveforms from Experiment 1 are also presented for visual comparison. To evaluate whether participants' P2 amplitude showed an overall increase from pretest to posttest, we conducted a 3 (group: progressive, constant, control) \times (2) (test: pretest, posttest) mixed analysis of variance (ANOVA) on the mean P2 amplitude across all deviant repetition rates. We found a significant main effect of test, $F(1, 24) = 17.03, \eta_p^2 = 0.42$; no other effect was significant. The mean pretest and posttest P2 amplitudes were further examined through a planned contrast for each group. This revealed a significant difference for the progressive and constant group, $t(8) = 3.78$ and $2.61, ps = .005$ and $.031$ respectively, but not for the control group. The group \times test interaction was not significant. The mean pretest and posttest P2 amplitude by group are shown in Figure 6.

Before further examining the effect of training on P2 amplitude, we evaluated the correlation between P2 difference scores and pretest amplitude within each group². The correlation coefficient was positive for both the progressive and the constant groups, $r(7) = .52$ and $.35, ps = .146$ and $.352$, respectively. It was negative for the control group, $r(7) = -.57, p = .104$. Although none of these within-group correlations was statistically significant, the pooled correlation between the progressive and constant group showed a significant positive correlation for the trained participants, $r(16) = .50, p = .034$. The P2 difference

²The same analysis was also conducted in Experiment 1, and the correlations between pretest P2 amplitude and P2 difference scores remained non-significant even after the trained groups were pooled to increase power.

scores were submitted to a 2 (group: progressive, constant) \times (7) (deviant repetition rate: 2, 4, 6, 8, 10, 11, 12 Hz) mixed ANCOVA. Pretest P2 amplitudes at all deviant rates were used as covariates to rule out the effect of pretest P2 amplitude on the difference scores. The control group was excluded because the participants' P2 amplitude was not significantly enhanced in the posttest, and because the correlation between pretest and difference score was in the opposite direction to that of the other two groups. This analysis revealed significant effects of group and group \times deviant rate interaction, $F(1, 8) = 6.54$ and $F(6, 48) = 2.34$, $\eta_p^2 = 0.45$ and 0.23 , respectively. The main effect of deviant rate was not significant, $F(6, 48) < 1$. These results indicate that, after controlling for pretest P2 amplitude, participants in the progressive group showed greater increases in P2 amplitude than did participants in the constant group. The significant interaction indicates that participants' P2 to different deviant sounds was differentially enhanced in the progressive and constant training groups.

To further evaluate these effects, we performed additional ANCOVAs separately on the slow (8 Hz and below) and fast (10 Hz and above) deviant sounds. A significant main effect of group was found for the slow deviant sounds, $F(1, 8) = 5.76$, $p = .043$, $\eta_p^2 = 0.45$. None of the other effects were significant in the two ANCOVAs. These results show that for slow deviant sounds, greater increments in P2 amplitude were found in participants in the progressive group than those in the constant group. However, no group difference was found for P2 evoked by fast deviant sounds.

General Discussion

In the present study, we found that participants trained to discriminate spectrotemporally complex FM sounds improved in their abilities to discriminate those sounds, and that training impacted the amplitude of electrophysiological responses evoked by FM sounds. After a single day of training, only students trained on a progressive schedule showed increased sensitivities to acoustic differences, as demonstrated by improved accuracy in the posttest compared to the pretest. In contrast, after eight days of training, participants in both training conditions exhibited an improved capacity to discriminate FM sounds after training. These improvements were not limited to the most difficult sound contrast used in training (11.5 versus 12 Hz); the improved perceptual capacity was also observed in response to other FM sounds that were not experienced during training.

The effects of training were different across experimental groups. Participants in both progressive training groups exhibited significantly more improvement than participants in the constant training groups. This differential effect of training regimen was consistent with our prediction, as well as with previous findings indicating that the learning of difficult discriminations can be facilitated by progressively requiring participants to detect finer perceptual discriminations (e.g., Tallal et al., 1996). Our results are also consistent with previous studies demonstrating that perceptual learning can occur in the auditory modality (Atienza et al., 2006; Demany, 1985; Demany and Semal, 2002; Foxton et al., 2004; Guenther et al., 1999; Kraus et al., 1995; Menning et al., 2000).

Training was associated with greater AEP wave amplitude measured in the posttest as compared to the pretest. This effect was found across multiple electrodes in Experiment 1. Similar to the behavioral results, participants in the progressive training groups exhibited a larger increase in P2 amplitude than participants in the constant training groups; the group by test interaction for the mean P2 amplitude was, however, only marginally significant ($p = .057$). The observed increments in P2 amplitude are consistent with previous studies of auditory plasticity using AEPs (Atienza et al., 2006; Reinke et al., 2003; Tremblay et al., 1997). Unlike past studies, which examined changes in P2 associated with the onsets of

transient sounds, the current study measured P2 evoked by changes in a continuous sound stream. Thus, the learning-related plasticity observed in the current study is specific to the detection of acoustic modulation.

Our results show that, compared to the fixed schedule of training used in the constant group, progressive training was associated with a higher degree of discrimination improvement as well as greater post-training P2 amplitudes. Adaptive training and fading techniques have been used in other studies of cortical plasticity (Tremblay and Kraus, 2002; Tremblay et al., 1997), and increased P2 amplitudes following training have also been observed. These previous studies have used progressive training to ensure rapid and appropriate learning but did not directly compare the sensitivity of P2 measures to effects produced by different types of training. Our study contributes to the literature in a unique way because it is the first to explicitly compare the electrophysiological correlates of learning through different training regimens, and to clearly demonstrate that changes in the amplitude of the P2 peak are sensitive to the relative effectiveness of progressive versus fixed training schedules. Knowing which training strategies are the most effective for the facilitation of learning and neural plasticity, and having easily measurable neural correlates that are sensitive to these differences is important because it can guide the development and implementation of learning-based therapeutic techniques.

In our study, we found that only a subset of deviant sounds (2–8 Hz) evoked a clear N1-P2 response, and that it was for those sounds that the P2 amplitude increased after training. This subset of sounds was not the same as the subset for which the behavioral discrimination improvements were observed (10–11.8 Hz), and most of those sounds were not part of the set of sounds used for training (except for 8 versus 12 Hz). Thus, it appears that the N1-P2 response was not homogeneously effective for the evaluation of neural plasticity related to the complete set of stimuli used in the present study. A possible reason for this could be that different neural mechanisms are in place for the processing of stimuli that have relatively slow sweep repetition rates (i.e., 2 – 8 Hz) versus those with faster repetition rates (10 – 12 Hz). Alternatively, the neural correlates of change detection may vary as a function of the degree of stimulus similarity.

What are the possible neural mechanisms that lead to a larger P2 amplitude following training? Although our study does not directly address this issue, some possible mechanisms include an increase in neural synchrony (Tremblay and Kraus, 2002), the recruitment of neighboring cells to respond to the learning stimuli (Reinke et al., 2003). (Elbert et al., 1995; Recanzone et al., 1993) and fine-tuning of the frequency response properties of the neurons responding to the training stimuli (Reinke et al., 2003). Neurons in the auditory cortex are sensitive to combinations of spectral and temporal properties of sounds (Orduna et al., 2001), and such sensitivities can be modified through learning (Linden et al., 2004). Therefore, changes in the spectrotemporal response properties of auditory cortical neurons could allow these neurons to carry out more refined discriminations involving spectrotemporally complex sounds, which could account for the increased P2 amplitude we observed following training.

In conclusion, we have shown that training involving complex sounds results in changes in perceptual and neural sensitivities, and that a combination of behavioral and electrophysiological techniques is a powerful tool to evaluate training-induced auditory plasticity. Our results contribute to the literature in several ways. First, we have demonstrated that different training regimens induce differential changes both behaviorally and physiologically. Second, the use of spectrotemporally complex, non-linguistic stimuli allowed us to explore neural mechanisms of auditory learning that may be independent of more specific language processing or pitch resolution mechanisms. Few previous studies

have evaluated the effects of learning and experience with amplitude and frequency modulated tones on evoked potentials (Draganova et al., 2009). Finally, the use of a modified oddball methodology for AEP collection involving continuous sound streams allowed us to explore the process of ongoing change detection and how training modifies this process.

Highlights

- Progressive training with complex sounds leads to more extensive behavioral and neural changes than constant training.
- Continuous sound presentations facilitate the measurement of learning-related plasticity of responses to change rather than responses evoked by transient onsets.
- Learning-related changes are evident after a single training session and can be directly observed using a single electrode.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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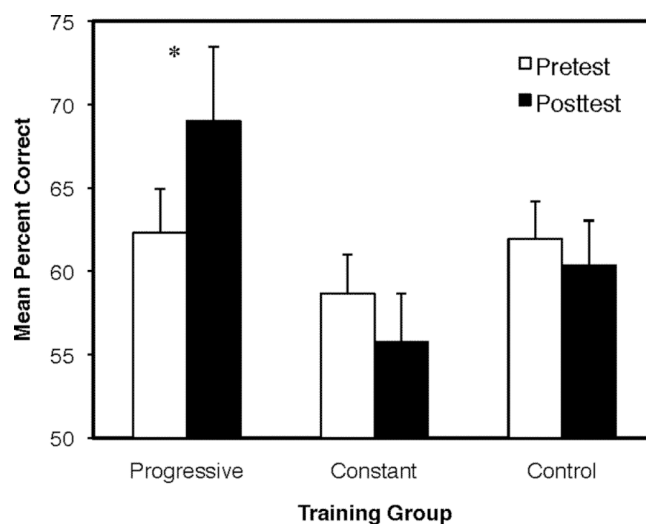


Figure 1.

The mean percent correct for the progressive, constant, and control groups in the behavioral pretest and posttest in Experiment 1 (one training session). Error bars represent standard errors of the means.

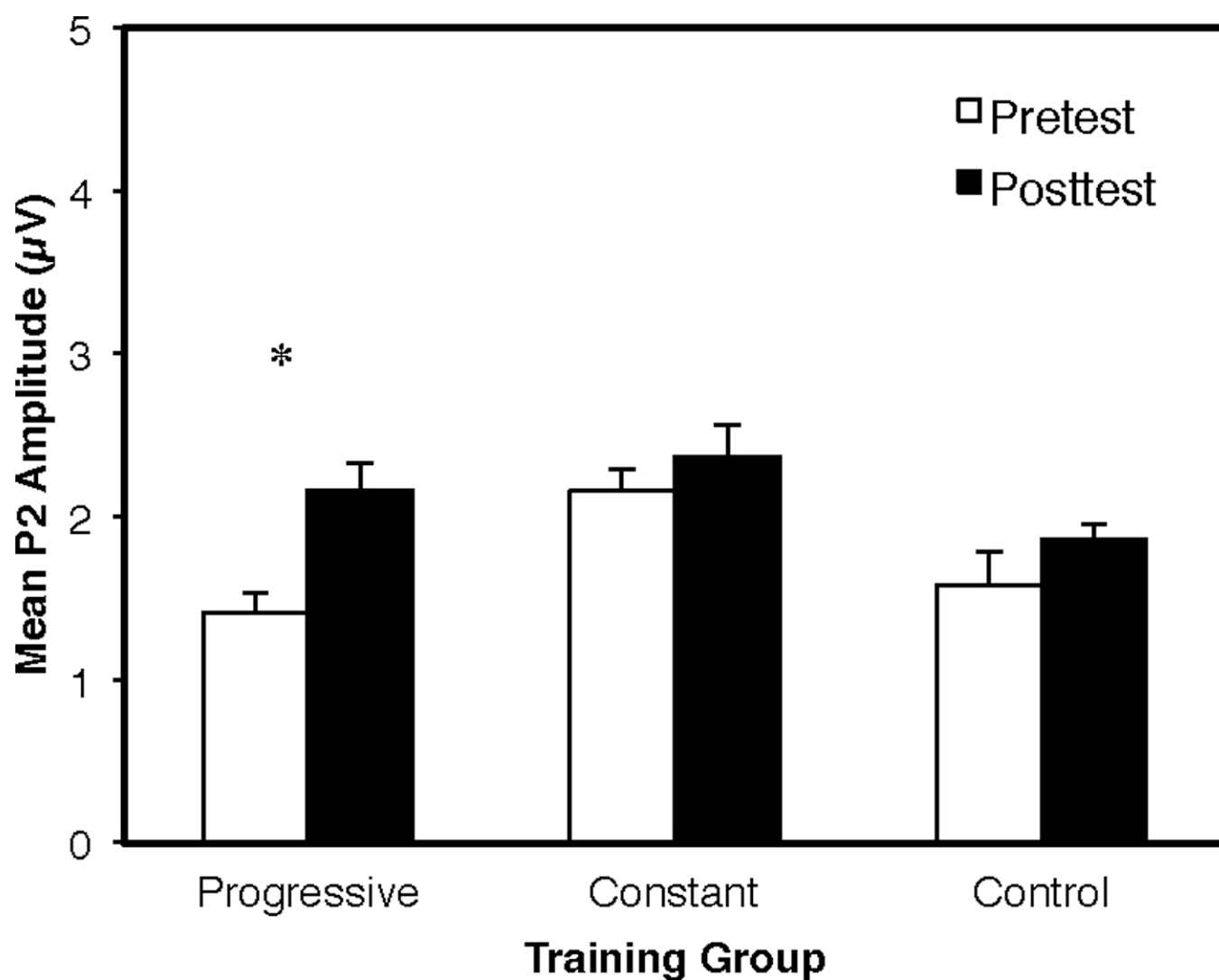
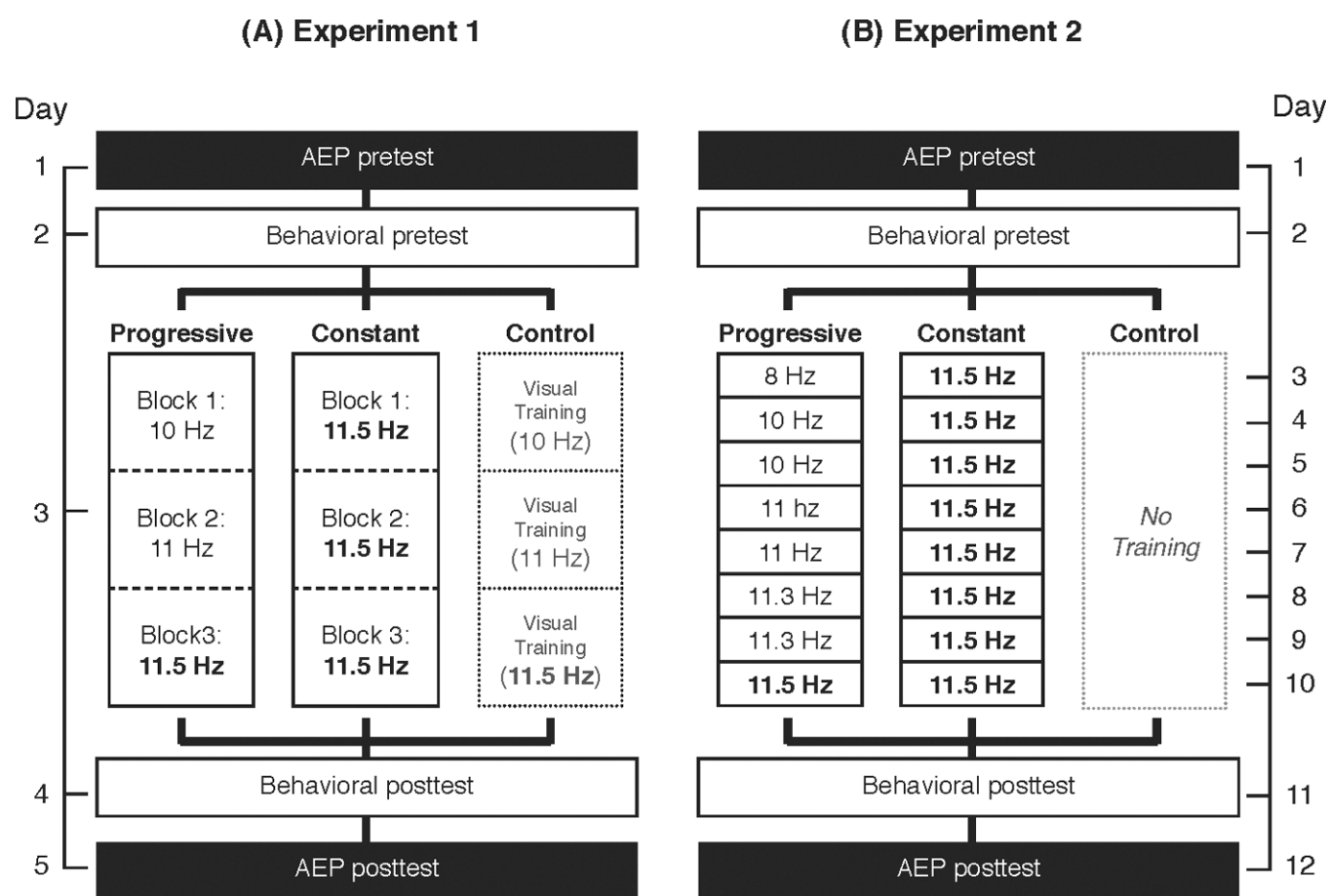


Figure 2. The mean P2 amplitude across all repetition rates and electrodes for the progressive, constant, and control groups in the AEP pretest and posttest in Experiment 1 (one training session).

**Figure 3.**

The design structure and time-line of (A) Experiment 1 and (B) Experiment 2. The noted repetition rate indicates the slow sound participants were trained to discriminate from the standard 12 Hz sound in the corresponding training block/session.

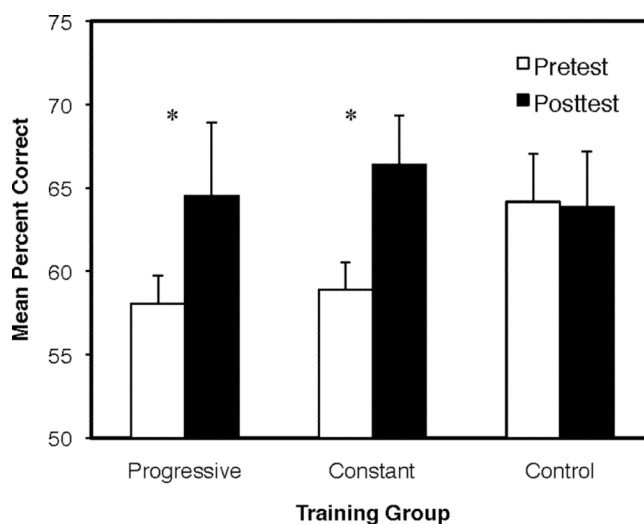
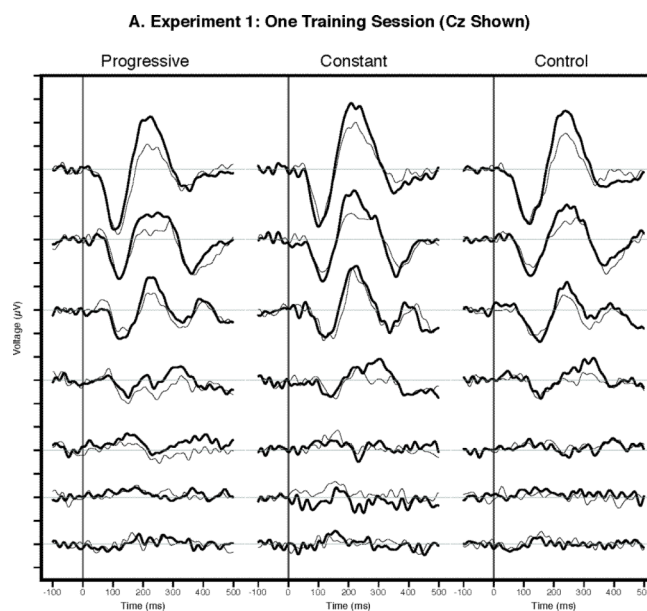


Figure 4.

The mean percent correct for the progressive, constant, and control groups in the behavioral pretest and posttest in Experiment 2 (eight daily training session). Error bars represent standard errors of the means.



B. Experiment 2: Eight Daily Training Session (at Cz)

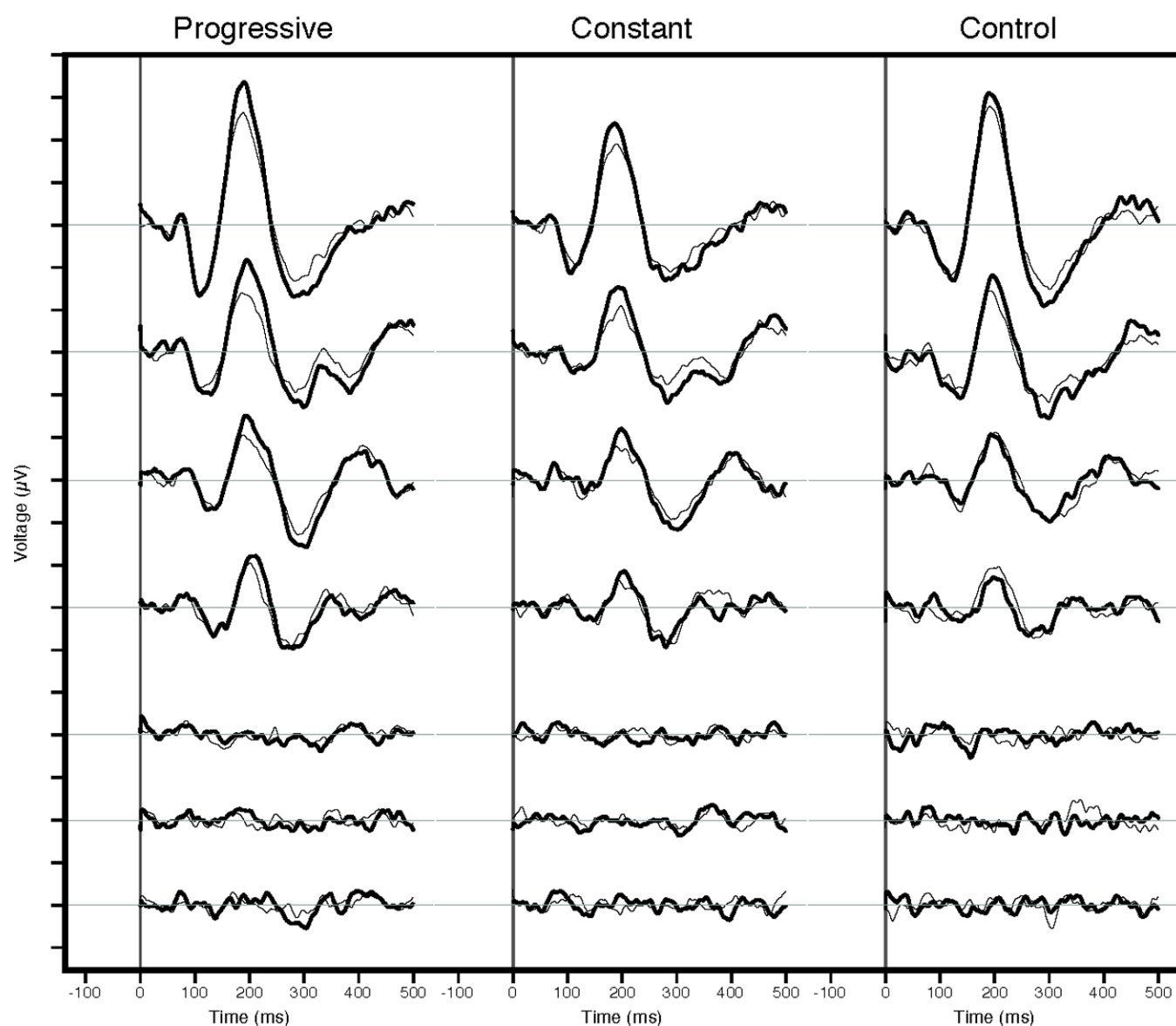


Figure 5.

The grand-average pretest and posttest waveforms at Cz for the progressive, constant, and control groups by deviant repetition rate (from top to bottom: 2, 4, 6, 8, 10, 11, 12 Hz) in (A) Experiment 1 and (B) Experiment 2.

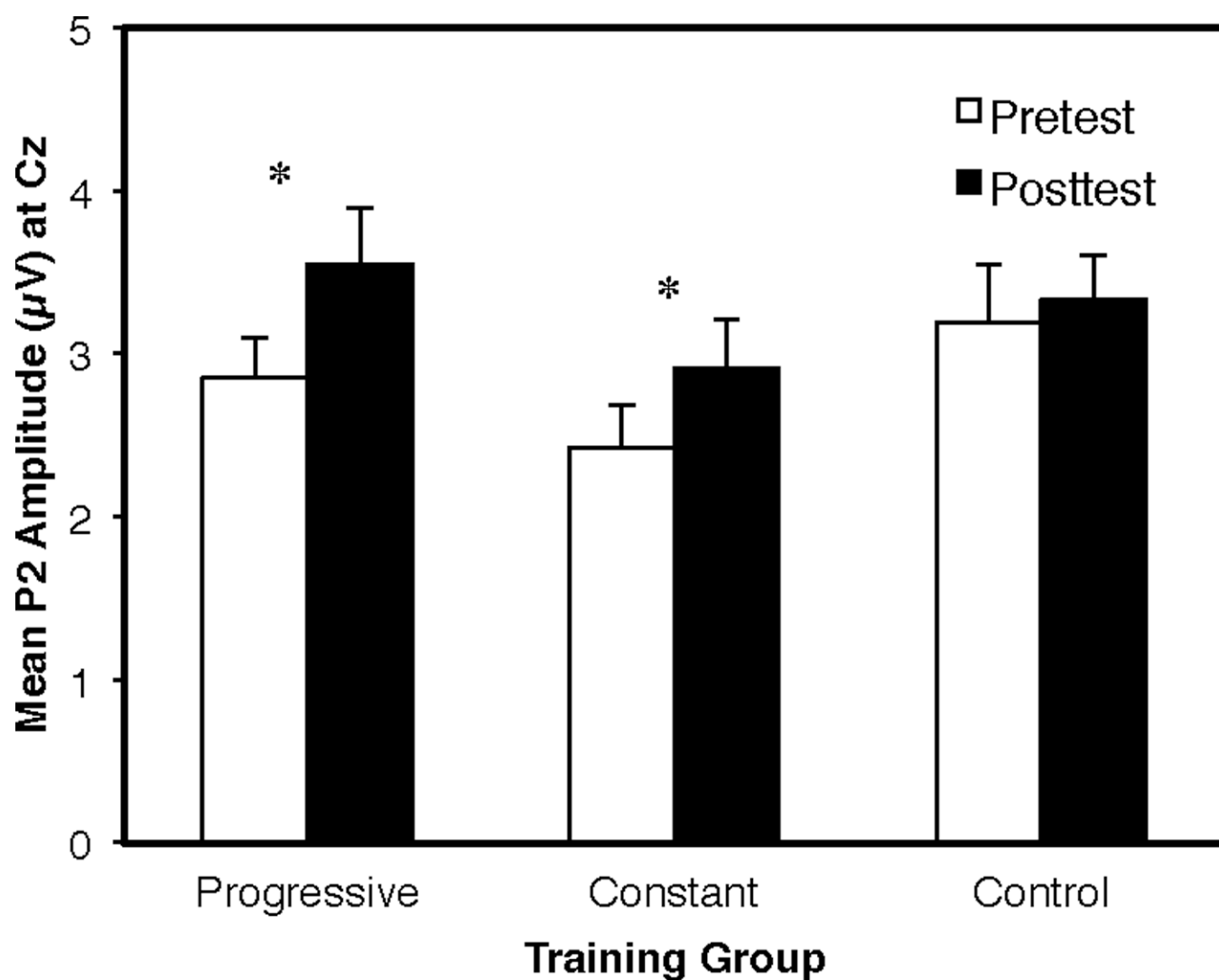


Figure 6. The mean P2 amplitude across the deviant repetition rates from Cz for the progressive, constant, and control groups in the AEP pretest (gray lines) and posttest (black lines) in Experiment 2 (eight daily training session).

Mean percent correct for discriminating FM sounds of different sweep repetition rates from a standard 12 Hz sound in pre- and post-tests for the progressive, constant, and control groups in Experiment 1 with one training session. Rates participants were able to differentiate reliably from the standard (accuracy > 48%) are presented in black. Rates participants were unable to reliably differentiate from the standard (accuracy < 48%) are presented in gray.

Table 1

Repetitions rate (Hz)	Progressive (n = 9)		Constant (n = 9)		Control (n = 9)	
	Pretest	Posttest	Pretest	Posttest	Pretest	Posttest
2	97	96	96	91	98	98
4	95	95	95	90	97	95
6	98	93	94	88	97	93
8	92	93	93	83	95	91
10	86	89	82	77	84	85
11	63	70	57	50	64	59
11.1	59	69	53	48	56	57
11.2	54	62	50	46	53	49
11.3	54	66	45	43	48	44
11.4	46	63	37	44	46	47
11.5	42	59	42	36	40	40
11.6	36	55	31	36	43	43
11.7	40	49	35	38	37	34
11.8	36	40	31	37	33	35
11.9	37	36	37	31	39	37

Table 2

Effects summary of the 3 (group: progressive, constant, control) \times (2) (test: pretest, posttest) \times (16) (electrode) mixed ANOVA on mean P2 amplitude averaged across all deviant repetition rates in Experiment 1.

Source of Variability	F	p	η_p^2
group	$F(2,24) = 4.844$	0.017	0.288
(test)	$F(1,24) = 20.305$	0.000	0.458
group \times (test)	$F(2,24) = 3.239$	0.057	0.213
(electrode)	$F(15,360) = 23.245$	0.000	0.492
group \times (electrode)	$F(30,360) = 1.650$	0.019	0.121
(test) \times (electrode)	$F(15,360) = 13.204$	0.000	0.355
group \times (test) \times (electrode)	$F(30,360) = 0.788$	0.782	0.062

Table 3

Effects summary of the 3 (group: progressive, constant, control) \times (7) (deviant repetition rate: 2, 4, 6, 8, 10, 11, 12 Hz) \times (16) (electrode) mixed ANOVA on P2 difference scores (posttest amplitude – pretest amplitude) in Experiment 1.

Source of Variability	F	p	η_p^2
group	F(2,24) = 3.239	0.057	0.213
(rate)	F(6,144) = 7.357	0.000	0.235
group \times (rate)	F(12,144) = 0.759	0.692	0.059
(electrode)	F(15,360) = 13.204	0.000	0.355
group \times (electrode)	F(30,360) = 0.788	0.782	0.062
(rate) \times (electrode)	F(90,2160) = 4.524	0.000	0.159
group \times (rate) \times (electrode)	F(180,2160) = 0.844	0.930	0.066

Table 4

Summary of the deviant rate contrasts (2, 4, 6 Hz versus 10, 11, 12 Hz) in P2 amplitude by electrode. A significant effect (shown in black) indicates that P2 amplitude at the corresponding electrode was modulated by the repetition rate of the deviant sound.

P2_(2, 4, 6 Hz) - P2_(10, 11, 12 Hz)	<i>p</i>	Electrode
5.386	0.000	F4
5.325	0.000	Fz
5.250	0.000	FCz
5.046	0.000	F3
4.886	0.000	C4
4.602	0.000	Cz
4.295	0.000	C3
3.713	0.002	F8
2.894	0.001	T4
2.498	0.001	Pz
2.212	0.001	P4
2.187	0.002	P3
1.204	0.034	T6
1.087	0.040	T5
0.932	0.131	O1
0.844	0.155	O2

Table 5

Mean percent correct for discriminating FM sounds of different sweep repetition rates from a standard 12 Hz sound in pre- and post-tests for the progressive, constant, and control groups in Experiment 2 with eight daily training sessions. Rates participants were able to differentiate reliably from the standard (accuracy > 48%) are presented in black. Rates participants were unable to reliably differentiate from the standard (accuracy < 48%) are presented in gray.

Repetitions rate (Hz)	Progressive (n = 9)		Constant (n = 9)		Control (n = 9)	
	Pretest	Posttest	Pretest	Posttest	Pretest	Posttest
2	98.89	94.44	98.33	95.56	99.17	98.89
4	98.06	94.19	98.06	95.00	98.61	98.33
6	96.39	91.94	96.94	94.72	98.61	97.5
8	96.67	89.44	95.00	93.61	98.89	96.67
10	83.89	78.81	85.00	88.33	92.50	89.44
11	56.67	63.11	55.83	72.50	65.83	63.89
11.1	<u>48.89</u>	59.83	51.67	70.00	66.11	61.67
11.2	47.78	60.66	51.67	63.61	63.33	62.22
11.3	41.94	56.33	<u>49.17</u>	60.83	55.00	61.11
11.4	42.78	57.50	41.39	58.06	52.78	<u>49.17</u>
11.5	38.06	58.06	42.22	55.28	<u>50.56</u>	47.78
11.6	36.94	<u>51.94</u>	39.17	<u>50.56</u>	41.39	46.11
11.7	35.56	44.97	37.78	40.00	38.89	40.28
11.8	36.11	42.98	30.28	41.94	36.94	33.89
11.9	38.06	38.06	36.94	37.50	32.17	36.67