Neurophysiological Consequence of Auditory Training: Subcortical and Cortical Structures

Madhok P.[1] & Sandeep M.[2]

Abstract

Earlier studies have shown that auditory system has capacity to reorganize and show plastic changes with auditory training. The changes have been demonstrated in both brainstem as well as cortical areas. However, the studies on the effect of training on brainstem structures are equivocal and fail to show any conclusive findings. One possible reason for this could be lesser number of sessions of training. Hence, the present study was aimed to see the effect of long term auditory discrimination training on brainstem and cortical responses to speech. To examine this, late latency and brainstem responses were recorded for speech stimulus before, during and after a stipulated period of auditory training in ten normal hearing subjects. Subjects were trained for frequency discrimination, intensity discrimination and temporal modulation identification for 33 sessions. Late latency and brainstem responses were recorded 5 times during the course of training. The results showed training related improvement in both brainstem and cortical responses evidencing neural plasticity secondary to auditory training in adulthood. However, plastic changes are slow in the brainstem compared to cortical areas.

Key words: *Auditory training, neural plasticity, discrimination, temporal modulation.*

The physiological representation of sound has been reported to alter with training exercises (Kraus & Disterhoft, 1982; Weinberger, Hopkins, & Diamond, 1984). Mechanisms of plasticity have traditionally been ascribed to higher-order sensory processing areas such as the cortex, whereas early sensory processing centers have been considered largely hard-wired. In agreement with this view, the auditory brainstem has been viewed as a non plastic site, important for preserving temporal information and minimizing transmission delays. However, recent results from animal models and human studies have revealed remarkable evidence for cellular and behavioral mechanisms for learning and memory in the auditory brainstem. However, two series of observations have led to reevaluation of these views. The first is that long-term synaptic and intrinsic plasticity do occur in some auditory brainstem nuclei. Second, electrophysiological studies in humans have uncovered new forms of learning and behavioral plasticity that are mediated by auditory brainstem structures. These findings establish a new role for the auditory brainstem and its modification by experience. Synchronized neural activity in response to sounds can be measured in humans by means of auditory evoked potentials. Simple (brief nonspeech) stimuli evoke an orderly pattern of responses from the auditory brainstem nuclei. The auditory brainstem response (ABR) is a noninvasive measure of far-field representation of stimulus-locked, synchronous electrical events. In response to an acoustic signal, a series of potential fluctuations measured at the scalp provides information about the functional integrity of brainstem nuclei along the ascending auditory pathway, making it a widely used clinical measure of auditory function. The frequency following response (FFR), a component of the ABR that occurs in response to a periodic stimulus, is well suited for examining how speech elements are encoded subcortically.

Krishnan and colleagues were the first to demonstrate that language experience affects brainstem activity by showing that speakers of tonal languages have enhanced neural representation of pitch (Krishnan, Xu, Gandour, & Cariani, 2005). Russo, Nicol, Zecker, Hayes, & Kraus (2005) also evaluated effect of auditory speech discrimination training for eight weeks of one hour each day. The brainstem and cortical responses verified tonically encoding periodic features of the stimulus in FFR, which were in fact, sensitive to longer duration of training. In contrast Kraus, McGee, Carrell,, King, Tremblay and Nicol (1995), showed no significant change in V peak post fifteen days of training.

FFR is a tool very well suited to reflect encoding of speech specific cues sub cortically. It reflects synchronized activity of axonal and dendritic potentials generated by neurons in LL/IC of the brainstem (Smith, Marsh, & Brown, 1975). But whether the physiologic changes could be attributed to, dendritic branching or, malleability of neurons for processing the stimulus, post training or, the time course of listening training (short term or long term) on subcortical structures, are yet to be known.

Thus it is evident that auditory system is quite responsive to training. There is common consensus that cortical structures show training related improvement in their physiology. But, there are

[1] e-mail: madhokpriyanka@gmail.com, [2] Lecturer in Audiology, AIISH; email: msandeepa@gmail.com

equivocal studies with respect to brainstem structures. Earlier evidence suggests that training induced changes are observed only in the upper brainstem and higher structures (Hayes, 2003). Though earlier articles have stated that the brainstem structures are resistant to later plastic changes, no physiological reasoning has been explained for this. Because most of the earlier studies which report of absence of plastic changes in brainstem involved training duration of less than twenty sessions, brainstem responses have probably not shown any significant changes. Otherwise, considering that the structure of the nerve fiber is not very different between brainstem & cortical areas, plastic changes secondary to auditory training should be observed in both the areas. Hence, there was a need to study the plastic changes in brainstem as well as cortical potentials with auditory training. Furthermore, most of the earlier studies are on children while the present study we aim to study the plastic changes in adulthood. Hence the aim of the present study was to investigate the effect of auditory discrimination training on brainstem and late latency responses to speech.

Method

The present study used time series design and attempted to verify the effect of training on the neural plasticity of the auditory system. The following method was adopted in the study. The experiment involved 3 components; 1) Generation of stimulus; 2) Auditory training and 3) Recording of auditory brainstem and cortical potentials.

Generation of stimulus: In the present experiment, it was aimed to auditorily train the subjects for frequency, intensity and duration discrimination. Hence, stimulus pairs that differ in their frequency, intensity and duration were generated.

Stimuli for frequency and intensity discrimination: Pure tones of different frequencies were generated using adobe audition software (ver. 3) Pure tones of 500 Hz, 1000 Hz and 2000 Hz were considered as reference tones while the other tones generated were variants of these reference tones. The variant tones varied in their frequency from 1 Hz to 30 Hz in 1 Hz steps. The reference tone was combined with any of their variant tones to make a block of three tones. In each block, two stimuli were same in frequency and one was different. The intensity was same in all the three tones of a particular block. The representative stimulus blocks with 10 Hz variance for 500 Hz, the reference frequency (RF) is shown in the example:

RF-500Hz:

block 1	500 Hz	G	500 Hz	G	510 Hz
block 2	500 Hz	P	510 Hz	P	500 Hz
block 3	510 Hz	A	500 Hz	A	500 Hz

⟵ 1.5 ➡ 1s ➡ 1.5s ➡

For intensity discrimination, pure tones for intensity discrimination were generated using a calibrated audiometer (Orbitter 922). At a particular frequency (among 500 Hz, 1000 Hz & 2000 Hz) the reference intensity was taken as 80 dB HL. The tones varied in their intensity from 1 dB to 10 dB in 1dB steps from 80-90 dB HL. The reference intensity (80 dB HL) was combined with any of their variant intensity (81-90 dB HL) to make a block of three tones using adobe audition software (ver. 3). In each block, two stimuli were same in their intensity and one was different. The frequency was same in all the three tones of a particular block. All the stimuli were generated with sampling rate of 44,100 Hz and 16 bit resolution. The total duration of each block was 6.5 seconds in which the duration of each stimuli was 1.5 seconds while the inter stimulus interval was 1 second.

Stimuli for Temporal Modulation: A computer with DaqGen software was used to generate the amplitude and frequency modulated white noise. DaqGen is a signal generator portion of the upcoming Daqarta (Data Acquisition & Real-Time Analysis) for Windows. This particular software was chosen because of 2 reasons: one, it allows continuous signal generation with fine frequency resolution. Second, depth of modulation and the frequency of modulation could be independently controlled. The software uses the following expression to modulate the signal: m (t) = [1 + m (sin2iifmt)]* n (t), where m = modulation index ($0<m<1$): when m = 1, the wave is said to be 100% modulated. Fm = modulation frequency and n (t) = wide band noise. The depth of modulation was varied in increments of 5% at 5 modulation frequencies: 8, 16, 32, 64 and 128 Hz. This was an online test and stimuli were not stored on a disc.

Auditory Training

Subjects: Ten subjects in the age range of 18-30 years participated in the auditory training. The participants were bachelor's students of Speech and Hearing and were blindfolded to the purpose of the study. They had normal intelligence and good academic performance. They did not have any past or present history of otological abnormalities and/or neurological deficits. Normal hearing sensitivity was confirmed on pure tone audiometry using a calibrated diagnostic audiometer (Grandson Stadler-61). The subjects had pure tone thresholds within 15 dB HL at octave frequencies between 250 Hz and 8 kHz (Goodman, 1965). Speech identification scores of all ten subjects were above 90% in quiet.

Middle ear functioning was assessed on tympanometry using GSI Tympstar immittance meter. All the subjects had 'A' type tympanogram with acoustic reflex thresholds at sensation levels of 70 to 95 dB HL. In the auditory training, the subject's task was primarily discrimination. However, in some instances identification was also required. Prior to inclusion, a written consent was taken from each subject after explaining the experimental protocol.

Training Procedure: Each subject underwent training for a total of thirty three sessions. Auditory training was given for duration of one hour every day. Pure tones and white noise were used for the training. Each session was divided into 3 sub sessions: 1) Training on Frequency discrimination (approx 15-20 min); 2) Training on Intensity discrimination (approx 10-15 min); and 3) Training on Temporal modulation (approx 20 min).

Discrimination Training for frequency and intensity discrimination and temporal modulation identification: Auditory stimuli were presented binaurally through headsets. The task of the subject primarily was to discriminate the tones differing in frequency and identify which tone in the block was different.

The difference in frequency varied from 1 Hz to 30 Hz. Initially training began with a frequency difference equal for their DLF and 1 Hz below their DLF. Each frequency difference could be presented in three different blocks as shown in the example earlier. That is, the variant frequency could be the first tone, second tone or the third tone in a block. Each of the three blocks were presented three times randomly which made nine-time presentation of each variant frequency. In each reference frequency, eighteen blocks were presented for training, of which nine blocks had frequency difference equal to subject's DLF while the other nine blocks had frequency difference that is 1 Hz below subject's DLF. The order of blocks was randomized. If the subjects were not able to discriminate, they were assisted through cueing. On completion of eighteen blocks, the performance was scored and the subjects were given feedback about their performance. When a particular subject scored >90% at a particular frequency difference, 1 step below that frequency difference was targeted in training. Subjects were allowed to take as much time as needed for the task. The identification score in each session was noted down in order to monitor the subject's progress. In each session, the time spent for training of frequency discrimination was approximately 15-20 min.

Same procedure was used for intensity discrimination training with difference in intensity varied from 1 dB to 10 dB. Initially training began with an intensity difference equal to their DLI and 1 dB below their DLI. For temporal modulation training, the task of the subject primarily was to identify the presence/absence of modulation in white noise. The white noise was modulated at different modulation frequencies; 8 Hz, 16 Hz, 32 Hz, 64 Hz and 128 Hz. The depth of modulation was varied in increments of 5% initially and the minimum modulation depth (TMTF) for white noise was found for each subject. Initially training began with the modulation depth equal to subject's modulation threshold at a particular modulation frequency. Each block in temporal modulation training involved presentation of ten stimuli where, five were modulated at modulation threshold of the subject while five were not modulated.

Recording of Auditory Brainstem and Cortical Potentials: Brainstem and cortical potentials were recorded after every ninth session of training and immediately after the last session of training. The recordings were done in a sound treated room where the noise levels were within permissible limits (ANSI, 1991; S3.1). Speech Evoked ABR and Long Latency Responses (LLR) were recorded using stimulus and acquisition parameters mentioned in Table 1 and 2 respectively.

Procedure

Auditory Brainstem Responses (ABR) and LLR were recorded using Bio-logic Navigation Pro with Biomark software (version 7). The clients comfortably sat on a reclining chair. The skin surface at the two mastoids (M1, M2), and upper forehead (Fpz) were cleaned with skin abrasive, to obtain skin impedance of less than 5 KΩ at each electrode site. The gold plated disc electrodes were placed with the help of skin conduction paste and surgical plaster was used to secure them tightly in the respective places. Subjects were instructed to relax and refrain from extraneous body movements to minimize artifacts. Single channel recordings were recorded ipsilaterally, using a vertical electrode montage.

Both the ears were tested in all the subjects. The responses were elicited by a 5 formant synthetic /da/ of 40 ms duration. The spectrum of the stimulus is as shown in the Figure 2.

Table 1.Stimulus and acquisition parameters used for recording speech evoked ABR

Acquisition parameters	
Epoch time	74.67 ms
Number of points	512
Maximum number of averages	3000
Pre stimulus time	-15 ms
Electrode impedance	<5 kOhms
Gain	100000
Low frequency filter	100 Hz
High frequency filter	3000 Hz
Artifact Rejection Threshold (ART)	23.80 µV
Stimulus parameters	
Stimuli	/da/
Ear	Right ear/left ear
Stimulus duration	40 ms
Transducers	Insert earphones
Polarity	Condensation/rarefaction
Intensity	90 dB SPL
Stimulus rate per sec	10.90
Number of sweeps	3000
Insert delay	0.80 ms

Table 2.Stimulus and acquisition parameters used for recording speech evoked LLR

Acquisition parameter	
Number of points	512
Maximum number of averages	200
Pre stimulus time	-15 ms
Electrode impedance	<5 kOhms
Gain	50000
Low frequency filter	1 Hz
High frequency filter	30 Hz
Artifact rejection Threshold (ART)	100 µV
Stimulus parameter	
Stimuli	/da/
Ear	Right ear/left ear
Stimuli duration	40 ms
Transducers	Insert earphones
Polarity	Alternating
Intensity	90 dB SPL
Stimulus rate per sec	1.1/s
Number of sweeps	200
Insert delay	0.80 ms

Response Analysis

Analysis of ABR: Good replicability of at least two waveforms was a prerequisite for considering the waveform for analysis. Brainstem responses elicited by speech were visually analyzed independently by two audiologists who were experienced in the area of electrophysiology. Both transient and sustained elements of the responses were analyzed. In the transient responses, the peak latency of wave V, A, and the peak to peak amplitude from V-A were noted from each individual wave. The sustained response was analyzed on Fast Fourier Transformation (FFT) and Brainstem Toolbox was used for this purpose. Brainstem Toolbox is a collection of MATLAB functions (m-files). Most can be invoked from the command line, but to take fullest advantage of the Toolbox, the GUI was to be used. The m-files that compose the "guts" of the program, reside in the program files folder. The time RMS amplitude was obtained for a time range of 11.4 ms to 40.6 msec. The amplitude at fundamental frequency (F0) and the first formant frequency (F1) were derived from FFT and co relational analyses. The frequency range that was used in assessing spectrum of response were centered at F0 (103-121), F1 (454-719) and F2 (721-1155). Since F2 is not coded precisely at brainstem level hence it was not considered for the analyses.

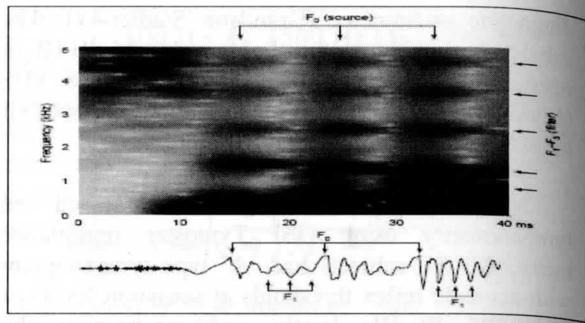

Figure 1./da/ stimulus of 40 ms duration used for recording brainstem and cortical potentials (courtesy Nina Kraus, NWU, Chicago).

Analysis of LLR: As in brainstem responses, good replicability of at least two waveforms was a prerequisite for considering the waveform for analysis. LLR elicited by speech was visually analyzed to record peak latency of wave P1, N1, P2 and N2 whereas amplitudes of P1N1 & N1P2 complex were obtained.

Results

Statistical Package for Social Sciences (version 16) software was used to carry out the statistical analysis. Descriptive statistics, Repeated measures ANOVA and Bonnferoni multiple comparison test were the statistical tests used.

The Effect of Auditory Discrimination Training on Brainstem Responses to Speech

Results of Onset Response: Brainstem responses were recorded on 5 days during the course of training. Both onset and sustained responses were analyzed. In the onset responses, latency of wave V and A and, the peak to peak amplitude (from V to A) were analyzed. The mean and standard deviation (SD) of latency and amplitude obtained from ten subjects are given in Table 3. The data is compiled separately for the five successive recordings (baseline-first, after 9th session-second, after 17th session-third, after 25th session-fourth and after 33rd session-fifth).

Table 3. The Mean and standard deviation (SD) of latency of V, A and V to A peak to peak amplitude in the five successive recordings

Recordings	Latency of wave V (ms)	Latency of wave A (ms)	Amplitude (V to A) (μv)
	Mean (SD)	Mean (SD)	Mean (SD)
First	6.48 (0.35)	7.59 (0.41)	0.27 (0.10)
Second	6.40 (0.33)	7.44 (0.37)	0.29 (0.10)

From the data given in Table 3, it can be inferred that training positively influenced the mean latency of wave V and mean peak to peak amplitude of the wave V to A. As the number of training sessions increased, the mean latency of wave V reduced and mean amplitude of V to A increased. However, no such trend was seen in the mean latency of wave A.

To see within subject effect of training and to see whether there was a statistically significant difference across recordings, repeated measure ANOVA was done. Results showed that there was a significant difference in the mean latency of wave V, [F (4, 76) = 2.956, p<0.05] and mean peak to peak amplitude of V to A, [F (4, 76) = 7.402, p<0.001] across the five recordings. However, there was no significant difference (p>0.05) in the mean latency of wave A across five recordings. Because there was a significant main effect of training on the onset responses, pair-wise comparison between the recordings was tested with Bonnferoni multiple comparison test. Results of Bonnferoni multiple comparison test are depicted in Table 4 & 5. The shaded portions depict the pairs which are significantly different from each other and the unshaded portions depict the pairs which are not significantly different from each other.

Table 4. *Pair-wise comparison of mean latency of wave V*

Recordings	1	2	3	4	5
First (1)	NS	NS	NS	NS	S
Second (2)	NS	NS	NS	NS	NS
Third (3)	NS	NS	NS	NS	NS
Fourth (4)	NS	NS	NS	NS	NS
Fifth (5)	S	NS	NS	NS	NS

*Note: **S** - p<0.05; **NS** - p>0.05*

Table 5.Pair-wise comparison of mean peak to peak amplitude of V to A

Recordings	1	2	3	4	5
First (1)	NS	NS	NS	NS	S
Second (2)	NS	NS	NS	NS	NS
Third (3)	NS	NS	NS	NS	NS
Fourth (4)	NS	NS	NS	NS	NS
Fifth (5)	S	NS	NS	NS	NS

*Note: **S** - p<0.05; **NS** - p>0.05*

Results of sustained responses: Fast Fourier transformation (FFT) was carried out on the sustained responses using Brainstem Tool Box. This toolbox presents the results of these analyses in a single report that consists of F0 amplitude and F1 amplitude derived from the responses. This was designed to analyze the periodicity in the brainstem responses. The data for amplitude of F0 and F1 is compiled separately for the five recordings (baseline-first, after 9th session-second, after 17th session-third, after 25th session-fourth and after 33rd session-fifth). The mean and standard deviation (SD) of F0 & F1 amplitude obtained from ten subjects are given in Table 6.

Results showed that there was a significant difference in the mean amplitude of F0, [F (4.76) = 28.113, p<0.001] and F1, [F (4.76) = 13.726, p<0.001] across the five recordings. Because there was a significant main effect of training on sustained responses, pair wise comparison between the recordings was tested on Bonnferoni multiple comparison test. The results of pair-wise comparison are depicted in Table 7 and 8.

Table 6. The Mean and standard deviation (SD) of amplitude of fundamental frequency (F0) & first formant frequency (F1)

Recordings	Amplitude of F0 (arbitrary dB)	Amplitude of F1 (arbitrary dB)
	Mean (SD)	Mean (SD)
First	2.52 (0.95)	0.71 (0.40)
Second	3.77 (1.57)	0.83 (0.33)
Third	4.64 (1.91)	0.90 (0.46)
Fourth	4.63 (2.00)	1.06 (0.29)
Fifth	6.04 (1.92)	1.12 (0.20)

Table 7.Pair-wise comparison of mean F0 amplitude

Recordings	1	2	3	4	5
First (1)	NS	S	S	S	S
Second (2)	S	NS	NS	NS	S
Third (3)	S	NS	NS	NS	S
Fourth (4)	S	NS	NS	NS	S
Fifth (5)	S	S	S	S	NS

*Note: **S** - $p<0.05$; **NS** - $p>0.05$*

Table 8.Pair-wise comparison of mean F1 amplitude

Recordings	1	2	3	4	5
First (1)	NS	NS	NS	S	S
Second (2)	NS	NS	NS	S	S
Third (3)	NS	NS	NS	NS	S
Fourth (4)	S	S	NS	NS	NS
Fifth (5)	S	S	S	NS	NS

*Note: **S** - $p<0.05$; **NS** - $p>0.05$*

The Effect of Auditory Discrimination Training on Late Latency Responses (LLR) to Speech

Latency of LLR: The mean and standard deviation (SD) of latency obtained from ten subjects are given in Table 9. The data is compiled separately for the five recordings.

To see the within subject effect of training and to see whether there was statistical difference in mean latency, repeated measure ANOVA was done.

Table 9.The Mean and standard deviation (SD) of peak latency of P1, N1, P2 and N2

Recordings	Latency of wave P1 (ms)	Latency of wave N1 (ms)	Latency of wave P2 (ms)	Latency of wave N2 (ms)
	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
First	98.76 (14.22)	117.69 (33.25)	173.70 (36.54)	259.01 (37.84)
Second	86.00 (26.08)	119.58 (40.86)	173.05 (44.99)	251.40 (57.00)
Third	71.37 (17.33)	109.97 (34.98)	178.23 (41.67)	265.18 (56.88)
Fourth	75.82 (23.40)	109.05 (29.56)	177.76 (31.40)	256.39 (49.97)
Fifth	67.46 (16.86)	100.83 (26.96)	173.90 (27.93)	243.82 (41.82)

Table 10.Pair-wise comparison of mean latency of P1

Recordings	1	2	3	4	5
First (1)	NS	NS	S	S	S
Second (2)	NS	NS	S	NS	S
Third (3)	S	S	NS	NS	NS
Fourth (4)	S	NS	NS	NS	NS
Fifth (5)	S	S	NS	NS	NS

*Note: **S** - $p<0.05$; **NS** - $p>0.05$*

Results showed that there was statistically significant difference in the mean latency of wave P1, [F (4, 48) = 19.215, $p<0.001$] and N1, [F (4, 76) = 4.356, $p<0.05$] across five recordings. On the other hand, significant differences were not observed in the mean latency of wave P2 & N2 across the five recordings. Pair-wise comparison on Bonnferoni multiple comparison for the above mentioned recordings for mean latency of wave P1 & N1 are shown in Table 10 & 11.

Successive pairwise comparison on Bonnferoni multiple comparison test showed that, there was a significant difference ($p<0.05$) in mean latency of P1 between first & third, first & fourth and first & fifth recordings. There were also significant differences between second & third and second & fifth recordings. The latency of wave N1 was significantly different ($p<0.05$) between first & fourth, first & fifth and second & fifth recordings No significant difference was observed for other pairs.

Table 11.Pair-wise comparison of mean latency of N1

Recordings	1	2	3	4	5
First (1)	NS	NS	NS	S	S
Second (2)	NS	NS	NS	NS	S
Third (3)	NS	NS	NS	NS	NS
Fourth (4)	S	NS	NS	NS	NS
Fifth (5)	S	S	NS	NS	NS

*Note: **S** - p<0.05; **NS** - p>0.05*

Table 12. The Mean and standard deviation (SD) of P1N1 and N1P2 peak to peak amplitude

Recordings	Amplitude of P1N1 (μv)	Amplitude of N1P2 (μv)
	Mean (SD)	Mean (SD)
First	1.51 (0.64)	1.96 (1.00)
Second	2.27 (1.00)	4.04 (1.82)
Third	2.92 (1.11)	4.89 (1.82)
Fourth	3.51 (0.91)	5.65 (2.28)
Fifth	3.92 (0.87)	5.94 (2.07)

Amplitude of LLR: The mean peak to peak amplitude across five recording is shown in table 12. From the mean data it can be inferred that training positively influenced the mean amplitude of P1N1 and N1P2 complex. As the number of training sessions increased, the mean amplitude increased consistently.

To see that the whether the observed differences in amplitude were statistically significant, repeated measure ANOVA was done. Results showed that there was a significant difference in the mean peak to peak amplitude of both P1N1 complex, [F (4, 48) = 29.478, p<0.001] and N1P2 complex, [F (4, 76) = 31.222, p<0.001] across five recordings. Following this, pair-wise comparison between the recordings was tested on Bonnferoni multiple comparison test. Pair-wise comparison for the above mentioned recordings are depicted in Table 13 & 14.

Discussion

Effect of auditory discrimination training on brainstem responses to speech: The present study incorporated a long term training program of thirty three sessions to evaluate the training related changes in brainstem and cortex. The results of brainstem responses showed that there was improvement in the latency, amplitude and phase locking properties of brainstem responses. This supports the notion that brainstem is not resistant to plastic changes but can be trained. The latency of the responses decreased and the amplitude of responses increased evidencing improvements in neural synchronization and neural conduction time.

Table 13.Pair-wise comparison of P1N1mean amplitude

Recordings	*1*	*2*	*3*	*4*	*5*
First (1)	NS	S	S	S	S
Second (2)	S	NS	NS	S	S
Third (3)	S	NS	NS	NS	S
Fourth (4)	S	S	NS	NS	NS
Fifth (5)	S	S	S	NS	NS

*Note: **S** - p<0.05; **NS** - p>0.05*

Table 14.Pair-wise comparison of N1P2 mean amplitude

Recordings	1	2	3	4	5
First	NS	S	S	S	S
Second	S	NS	NS	S	S
Third	S	NS	NS	NS	S
Fourth	S	S	NS	NS	NS
Fifth	S	S	S	NS	NS

*Note: **S** - p<0.05; **NS** - p>0.05*

However, the rate of training related changes was different within the components of brainstem responses. Sustained component of brainstem responses showed earlier change compared to the onset responses. Considering that FFR represents phase locking abilities of neurons while onset responses represent neural synchronization of nerve fibers, it can be inferred that phase locking can be trained easily compared to synchronizing abilities of neurons. Earlier studies in this direction have focused on only the onset responses and had given training for not more than twenty sessions. In the present study, it was noticed that the change in onset responses was evident only after twenty five sessions i.e., onset responses require more extensive training to show the changes which was not done in the earlier studies. This could be the reason for the present results not being in agreement with the studies in literature.

In the auditory system, the brainstem is uniquely organized to encode rapid timing changes in auditory signals. Auditory processing disorders in some of the language based dysfunctions like learning impairments; ADHD and dyslexia have been attributed to the deficits in the precision of neural encoding at the level of brainstem. In such a case the results of the present study are promising because auditory training has shown evidences of changes in neural timing.

Discrimination and identification tasks require temporal judgment and temporal resolution in the CANS. Transient acoustic events which are varied in frequency, intensity or duration evoke a pattern of voltage changes in the auditory brainstem. The significant increase in amplitude measure of onset as well as sustained responses could also be attributed to the presence of activity-dependent changes in the synaptic strength at the brainstem level. As reported by Krishnan et al (2005), the brainstem nuclei could represent the cellular changes that may underlie and support learning behavior in the present study.

Effect of auditory discrimination training on late latency responses (LLR) to speech: The present study also showed training induced changes at the cortical level. Latency as well as amplitude of late latency responses was found to be improved with training evidencing improvements in neural conduction time as well as neural synchronization. However, latency improvement was seen in P1 & N1 and not seen in P2 & N2. This could be because these potentials are generated from different generators. The generators of P1N1 (primary auditory cortex, thalamus and Heschels gyrus) are probably easier to train compared to the generators of P2 and N2. Collectively, these results suggest that the temporal relationship between learning and neurophysiological plasticity is variable and may depend on the relative difficulty of discriminations. However, it is possible that independent timing mechanisms exist for each frequency, but if a task does not require attending to a given frequency; all the circuits can undergo learning through top-down mechanisms. Similarly, studies in guinea pigs revealed a correlation between auditory receptive field plasticity and behavioral learning for an easy discrimination, whereas there was dissociation between behavior and cortical plasticity for a difficult discrimination (Edeline & Weinberger, 1993).

Results of the present study showed enhancement in both P1N1 and N1P2 complex. Among the latency and amplitude of LLR's, the mean amplitude showed much faster and rapid changes to training than latency. Increases in N1 and P2 amplitudes may reflect heightened sensitivity to what was once a subtle acoustic cue. Another reason that could be attributed to enhancement of amplitude complex is increased myelination of neuronal axons and/or the recruitment of additional neurons to existing generators. Further, in the present study, compared to the ABR, late latency responses showed earlier changes. Therefore it could be inferred that neurophysiological plasticity in the human auditory system is faster at cortical level than at brainstem level. This could be attributed of difference in the number of neurons between brainstem and cortical neurons. Because there is more number of neurons in the cortex, there is more scope for neural arborization and in turn plasticity. In fact, the combined results of Molchan, Sunderland, McIntosh, Herscovitch, & Schreurs (1994) & Schreurs, McIntosh, Bahro, Herscovitch, Sunderland, & Molchan (1997), indicate that auditory cortical plasticity can develop within minutes.

Furthermore, it could be inferred that the plastic changes at the brainstem and cortical structures, due to training, evidence generalization. That is, although non speech training was given to the ten subjects, responses elicited by speech stimulus showed improvement in processing. One could infer from these results that the plastic change is cue based and not confined to whether it is speech/non speech training.

From the results of the present study it can be concluded that training tunes both bottom-up and top-down neural mechanisms. Some changes are likely specific to the trained stimulus and some reflect more generalized processing. Here we conclude by stating that there are stimulus specific and non-specific effects of training that can be measured in humans, and that patterns of brain activity, as well as the presence or absence of brain-behavior relationships, can help define the underlying neural mechanisms affected by this type of training protocol. The reverse hierarchical theory suggests that learning consists of an attention-driven, task-dependent 'backward' search for increased signal- to-noise ratio, especially for perceptual tasks including cognitive influence. Studies on simple attributes of sound (pitch, duration) showed increased physiological response, improved response precision, and sharpening of receptive fields at the level of neurons and reorganization of cortical maps. Cognitive and sensory processes are thus inextricably linked, and scalp recorded brainstem and cortical responses may provide a comprehensive view of consequence of this process as a system in humans. It could be hypothesized that probably the cortical structures which are rapid to plastic changes are mediating and guiding the brainstem processing thus making it more plastic to auditory training.

Conclusions

From the findings of the present study it can be concluded that training related changes can be observd in both brainstem as well as cortical areas. These changes can be documented on electrohysiological data. However the plastic changes were seen earlier in cortical areas than brainstem areas.

References

American National Standards Institute (1991). "American National Standard maximum permissible ambient noise levels for Audiometric Test rooms". ANSI S3.1. (1991). New York: *American National Standards Institute.*

Gordon, M., & O'Neill, W. E. (2000). An extralemniscal component of the mustached bat inferior colliculus selective for direction and rate of linear frequency modulations. *Journal of Comparative Neurology, 426,* 165–181.

Kraus, N., & Disterhoft, J. F. (1982). Response plasticity of single neurons in rabbit auditory association cortex during tone-signaled learning. *Brain and Research, 246,* 205–215.

Kraus, N., McGee, T., Carrell, T. D., King, C., Tremblay, K., & Nicol, T. (1995). Central auditory system plasticity associated with speech discrimination training. *Journal of Cognitive Neuroscience, 7,* 25–32.

Kraus, N., McGee, T., Carrell, T., & Sharma, A. (1995). Neurophysiologic bases of speech discrimination. *Ear and Hearing, 16,* 19–37.

Krishnan, A., Xu, Y., Gandour, J., & Cariani, P. (2005). Encoding of pitch in the human brainstem is sensitive to language experience. *Cognitive Brain Research, 25,* 161–168.

Molchan, S. E., Sunderland, T., McIntosh, A. R., Herscovitch, P., & Schreurs, B. G. (1994). A functional anatomical study of associative learning in humans. *Proc Natl Acad Sci USA, 91,* 8122--8126.

Rosen, S. (1992). Temporal information in speech: acoustic, auditory and linguistic aspects. *Phil Trans R Soc Lond, 336,* 367–373.

Russo, N. M., Nicol, T. G., Zecker, S. G., Hayes, E. A., & Kraus, N. (2005). Auditory training improves neural timing in the human brainstem. *Behavioural Brain Research, 156,* 95–103.

Weinberger, M. N., Hopkins, W., & Diamond, D. M. (1984). Physiological plasticity of single neurons in auditory cortex of the cat during acquisition of the pupillary conditioned response: I. Primary field (AI). *Behavioral Neuroscience, 98,* 171–188.

Wong, P. C. M., Nusbaum, H. C., & Small, S. L. (2004). Neural bases of talker normalization. *Journal of Cognitive Neuroscience, 16,* 1173–1184.