

Research article

Auditory detection learning is accompanied by plasticity in the auditory evoked potential

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ABSTRACT

Auditory detection can improve with practice. These improvements are often assumed to arise from selective attention processes, but longer-term plasticity as a result of training may also play a role. Here, listeners were trained to detect either an 861-Hz or 1058-Hz tone (counterbalanced across participants) presented in noise at SNRs varying from -10 to -24 dB. On the following day, they were tasked with detecting 861-Hz and 1058-Hz tones at an SNR of -21 dB. In between blocks of this active task, EEG was recorded during passive presentation of trained and untrained frequency tones in quiet. Detection accuracy and confidence ratings were higher for trials at listeners' trained, than untrained-frequency (i.e., learning occurred). During passive exposure to sounds, the P2 component of the auditory evoked potential (~150–200 ms post tone onset) was larger in amplitude for the trained compared to the untrained frequency. An analysis of global field power similarly yielded a stronger response for trained tones in the P2 time window. These effects were obtained during passive exposure, suggesting that training induced improvements in detection are not solely related to changes in selective attention. Rather, there may be an important role for changes in the long-term neural representations of sounds.

1. Introduction

Experience can alter performances in a number of different listening tasks. For instance, practice can improve detection thresholds [1,2], increase sensitivities to differences between simple [3] and complex sounds [4–6], and alter spatial acuities [7,8]. Given the variety of tasks that show this *perceptual learning*, it is perhaps unsurprising that the processes behind experience-related changes in perception have been hotly debated (for review, see [9,10]).

Some view auditory perceptual learning as a process wherein individuals learn what acoustic features to selectively attend [11–13]. For instance, if frequencies near 1000 Hz are relevant for the task at hand, selectively attending to frequencies near 1000 Hz will lead to better acuity. Others posit that long-term changes to sensory representations and their read-out connections improve perception [9,14–18]. This could occur by means of an increase in the number of neurons coding for a particular feature (e.g., receptive fields shift from a best frequency of 750 Hz–2500 Hz [16]), neurons becoming more selective to inputs [19], or to associations between representations and decisional output being reweighted [9]. Indeed, such changes can be observed even under

anesthesia [20] and passive exposure to sounds (e.g. [4]).

Explanations of experience-related changes in auditory detection abilities have been weighted heavily towards the selective attention position. For instance, Zwillocki et al. [1] ascribed reduced attention as a “fairly straightforward” (p. 256) reason for decrements in detection threshold, and motivation as key to improving it. Tanner and Norman [36] had listeners detect a 1000-Hz tone in noise for hundreds of trials in which listeners were approximately 65 % correct. When the frequency of the tone was changed to 1300 Hz, performance was brought down to chance (~25 % correct). Performance promptly rose after subjects were informed of the frequency change, presumably because they recalibrated an attentional filter. More recent psychoacoustic works have also considered the possibility that learned changes in detection abilities are related to attention [12,21–23]. Notably, Jones et al. [12] trained listeners to detect 1000 Hz tones in 30-component multitone maskers (excluding frequencies in a 1/3 octave band surrounding 1000 Hz). Listeners' weights upon different frequency regions were estimated using logistic regressions, and it was found that weighting efficiency (i.e., the degree to which weights were optimal), increased over the course of training. Though the setting of such

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weights could reasonably result from several learning mechanisms (e.g., changes in attention, representation, or read-out connections; cf. [9,24]), those authors concluded that “selective attention underlies improvement” ([12]; pg. EL133).

Similar to the above-mentioned behavioral detection work, participants in this study were given training in a tone-in-noise task where the frequency of the presented tone was fixed. After training, participants were tested with both a trained frequency and a previously unheard novel frequency. We probed both accuracy and confidence in performance. Interleaved with these active blocks were passive blocks in which the same tones were presented, but participants were asked to ignore sounds while EEG was recorded. We expected post-training accuracy and confidence ratings for the trained frequency to be higher than the untrained frequency. That is, we expected to see evidence of learning in behavior. Analyses of the EEG time-locked to tone presentation in the passive blocks were used to covertly monitor cortical responses to trained sounds when individuals were not engaged in a task (i.e., when there was little motivation to selectively attend). Several studies of discrimination learning have shown auditory N1, P2, and global field power (GFP) to increase in amplitude as a result of discrimination training [4,5,25–29]. This is the case even when listeners are asked to ignore the sounds that are being presented to them during “passive” blocks (e.g. [4]). We expected that if detection learning is at least partially driven by processes outside the scope of selective attention, there should be differences observable in passive blocks.

2. Methods

2.1. Participants

Sixteen young adults with tested normal hearing (< 20 dB HL, 0.25 – 8-kHz) participated in this study for compensation. All participants gave signed informed consent. The study was approved by the U.S. Air Force Research Laboratory’s Wright-Site Institutional Review Board. Two listeners were dropped because of excessively noisy EEG data.

2.2. Apparatus

Participants were seated in a sound-attenuating booth. Sounds were presented diotically through earphones (ER-2; Etymotic Research, Elk Grove Village, IL, USA) at a level not exceeding 80 dB SPL. Experimental procedures were executed in MATLAB (Mathworks, Natick, MA). Timing of stimuli was controlled using a TDT system 3 real-time processor (RP2.1; Tucker-Davis Technologies, Alachua, FL).

2.3. Training

A two-interval two-alternative forced choice (2i-2afc) paradigm was used (See Fig. 1). On each trial, consecutive 2400-ms cosine-ramped (500-ms onsets and offsets) white noise sources were presented with a 100-ms gap between. These white noise sources were frozen across trials and participants to minimize acoustic trial-by-trial differences. An 80-ms pure tone was presented in one of the two noises, at either 861-Hz or 1058-Hz, and always at 1160 ms relative to noise onset. Participants were tasked with indicating which interval (referred to as masker

in instructions) contained the tone using the number pad on a computer keyboard. During testing, participants were also asked to rate their confidence on each trial on a 1–6 Likert scale. There were no response deadlines for the detection or metacognitive task (cf. [30]).

For half the participants, training involved detecting the 861-Hz tone. For the other half, training involved detection of the 1058-Hz tone. Participants underwent 8 blocks of 20 detection trials with feedback of correctness presented after responding in the detection task. From block 1 to block 8 the SNRs were: -10, -12, -14, -16, -18, -20, -22, and -24 dB. This fading from easy to hard SNRs was employed so that: 1) the demands of the task were made obvious to participants; and 2) perceptual learning would be effectively produced (for review, see [4,10,31]). All of training took place in a single session of ~ 30 min.

2.4. Testing

Testing procedures were carried out in a separate session on the day immediately following training. Testing involved two different protocols. The first protocol, which we refer to as “Active,” employed procedures similar to training. SNR was fixed at -21 dB, and trials contained the 861-Hz and 1058-Hz tones with equal *a priori* probabilities. In each block, participants completed 50 trials. Unlike training, no feedback was provided. There were 5 total active blocks (~ 125 trials per frequency; 250 trials total). Individuals were informed that there could be more than one tone frequency within a block. An active block lasted approximately 8 min.

The second protocol, which we refer to as “Passive,” was characterized by 861-Hz and 1058-Hz tones presented in silence. Frequencies were varied within a block with equal *a priori* probabilities. Stimulus-onset asynchronies varied randomly between 350-ms and 850-ms. There were 5 blocks of 100 tone presentations (~ 250 per frequency; 500 total). Participants were asked to ignore the sounds and read material of their own choice during this period [32]. A passive block lasted approximately 1.5 min. Passive and active blocks were interleaved throughout the testing session. All together, including breaks in between blocks, data collection lasted ~ 50 min for the test.

2.5. EEG methods

EEG data (135 channels) were gathered at a 2048-Hz sample rate, 24-bit A/D resolution, and were referenced to the common-mode-sense driven-right-leg electrodes (CMS/DRL) of a BioSemi Active II system (BioSemi, Amsterdam, the Netherlands). Caps were used with 128 electrode positions arranged according to a BioSemi equiradial format. The additional 7 electrodes were placed on the nose tip, on lateral sides of the eyes, underneath eyes, and on the mastoids.

All data processing and analyses were performed using EEGLAB [33] and custom MATLAB scripts/functions. Data were re-sampled at 256-Hz (after applying an anti-aliasing filter), re-referenced to the average of mastoids, and digitally filtered with a zero-phase FIR high-pass (.25 Hz half-amplitude cutoff) and low-pass filter (56.25 Hz half-amplitude cutoff). Channels and portions of markedly noisy data were manually removed based on visual inspection. Independent component analysis (ICA) was run on the remaining continuous data. Independent component (IC) processes identified as eye- or muscle- movement artifacts (based on scalp projections, spectra, and time courses) were

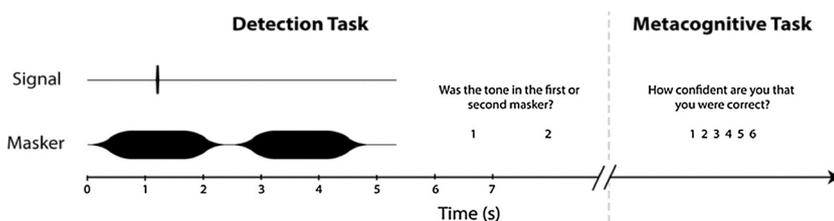


Fig. 1. Depiction of the active task used in training and testing. For training, the metacognitive portion of the task was absent.

removed from the data (i.e., the data were corrected for artifacts; cf [18,34]).

For AEP analyses, epochs were extracted from -0.15 to 0.3s surrounding onsets of tones in the passive blocks. Baselines were removed (-150 – 0-ms). Epoch voltage time-courses were averaged to make AEPs. For analyses of the AEP, we averaged AEPs across a central cluster of electrodes where the AEP is typically measured (see Fig. 2a for electrode locations). Amplitudes of P1, N1, and P2 components were extracted using mean voltages within time-windows selected based on AEPs averaged across trained and untrained frequencies. These windows were 40 – 80-ms, 90 – 110-ms, and 150 – 200-ms respectively. GFP was also analyzed by taking the standard deviation of voltage across electrodes for each time-point in these AEPs. GFP reflects how strong a potential is across all electrodes in the electrode montage and can be more sensitive to differences between conditions, especially when using high-density montages such as the one used here [35]. GFP was analyzed in the same time windows as the AEP.

3. Results

3.1. Behavioral data

Table 1 presents accuracy (proportion correct) for trained and untrained frequencies in the test. Proportion correct was significantly higher for the trained compared to the untrained frequency, $t(13) = 3.41, p = .005$, Cohen's $d = 0.76$. Training therefore had the expected effect. Training had a similar impact on confidence ratings. That is, ratings of confidence were significantly higher for the trained compared to the untrained frequency, $t(13) = 3.86, p = .002$, Cohen's $d = 1.44$. In general, the behavioral data show strong effects of learning on detection accuracy and confidence.

3.2. Electrophysiology during passive exposure

Fig. 2a shows ERPs time-locked to trained (solid line) and untrained (dashed line) tone onsets. For both trained and untrained frequencies there were clear AEPs with middle latency Pa and Nb components, and the later P1, N1, and P2 components that were of interest here. Further, scalp maps shown in Fig. 2b display typical scalp distributions for P1, N1, and P2.

There were apparent differences between trained and untrained tone amplitudes observable in the AEP waveforms (Fig. 1a) and scalp maps (Fig. 2b). Paired-sample t tests revealed a significant difference for P2 amplitude, $t(13) = 2.26, p = .042$, Cohen's $d = .60$. Means for P1 and N1 were not significantly different between conditions, $t_s < 1.3$ ¹

Traces of global field power for trained (solid line) and untrained (dashed line) tones are shown in Fig. 3. Mimicking the AEP data, GFP in the P1 and P2 windows appeared to be strongest following trained compared to untrained tones. Paired-sample t tests revealed a significant difference for P2, $t(13) = 3.24, p = .006$, Cohen's $d = .87$. Mean GFP in the P1 and N1 time-windows were not significantly different between conditions, $t_s < 1.46$.

4. Discussion

We observed auditory detection training effects such that tones at a trained frequency were detected with greater accuracy and rated with greater confidence than tones at an untrained frequency. Accompanying these behavioral effects was a larger amplitude P2 in the

¹ An additional analysis at a cluster of frontal channels also failed to yield a significant difference for either P1 or N1, $t_s < 1.17$. For readers interested in AEPs from the active portion of this task, see Ball et al. [43] and Zakrzewski et al. [30].

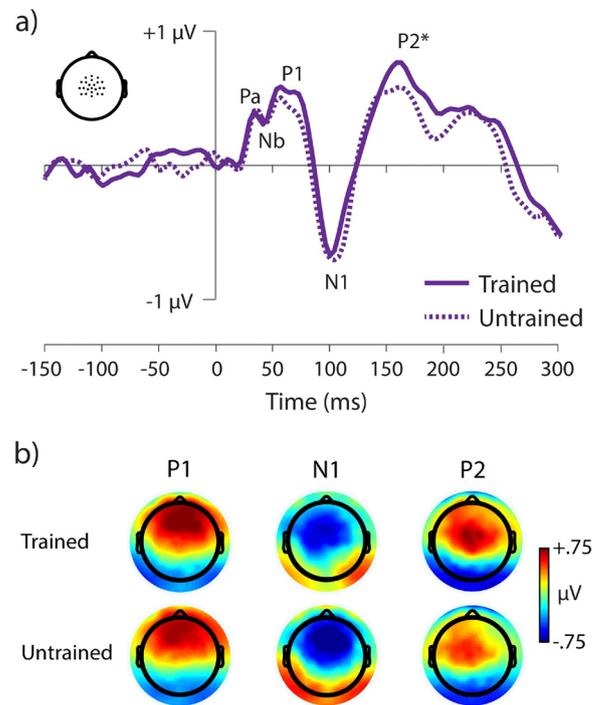


Fig. 2. (a) AEPs at the central cluster of electrodes for untrained (dashed line) and trained (solid line) tones presented during passive blocks. Components of the AEP are labeled. In the scalp image in the upper left corner, black dots represent the locations of electrodes within the central cluster. The asterisk marks a significant difference in component amplitude ($p < .05$) (b) Scalp maps of P1, N1, and P2 amplitudes for untrained and trained tones.

Table 1

Behavioral Data Summary.

	Proportion Correct	Confidence Rating
Trained Frequency	0.87 (.03)	3.69 (.31)
Untrained Frequency	0.74 (.04)	2.81 (.32)

Note. Values in parentheses represent standard error of the mean.

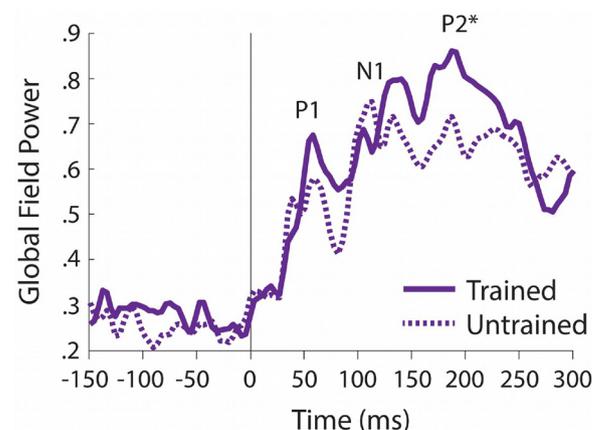


Fig. 3. Global field power time-locked to the onset of trained and untrained tones in passive blocks. The asterisk marks a significant difference for GFP in the P2 time-window ($p < .05$).

AEP for the trained compared to the untrained frequency, and a corresponding larger GFP in the P2 time-window. In other words, the response to trained sounds was stronger than the response to untrained sounds. This occurred under a condition of passive exposure. Many works (both early; [36], and current [12];) have assumed that

improvements in auditory detection are a result of selective attention. The significance of this work is that it suggests an additional role for learning-related changes in neural responses outside the scope of selective attention.

If learned improvements in auditory detection partially result from processes related to representational plasticity for experienced stimuli, this has important consequences for how explicit training regimens should be designed. Auditory detection sensitivities are critical for many occupations. For instance, survivability for military operators depends on the detection of threat signals (e.g., the sound of an enemy reloading) in noisy environments [37]. It has been repeatedly argued that listening training needs to be integrated into military training in order to maximize auditory situational awareness [37,38]. It is common to approach perceptual training design with the assumption that the brunt of learning involves knowing what to listen for ([11] [13];). For instance, some suggest to employ a few very easy trials to direct attention to relevant dimensions before switching to difficult trials [13]. However, recent work suggests that such protocols may not yield learning effects as strong as protocols that are designed to maximize the efficiency of representation-based learning processes [10,31]. Furthermore, in scenarios like those common in military operation, listeners may need to detect many different types of signals, or changes in signals, that have drastically different spectral profiles [37,39]. It would be difficult to employ an attentional filter that encompasses all signals of importance, while also filtering out unimportant signals. Work on auditory detection training should consider how different types of training constrain long-term plasticity rather than just momentary settings for attentional filters.

One important caveat to this work has to do with our assumption that selective attention was not being utilized in the passive protocol. Participants were instructed to ignore the sounds, and instead focus on reading material of their choosing. This is a common procedure in AEP studies [32]. There was little motivation to pay attention to sounds, and even less so to pay attention to sounds at one frequency over another. Nevertheless, we cannot definitively say that participants avoided paying attention to the trained frequency during passive EEG recordings. It is noteworthy that we observed no differences between trained and untrained frequencies for the N1. This is a component often associated with auditory selective attention (e.g., [40]). Further, other work suggests that attention leads to decreased P2 amplitudes [41]. We thus observed the opposite of what would be expected if trained sounds received more attention. We hypothesize that the same result should hold when attention is diverted from the frequency dimension of tones to some other dimension during EEG recording (e.g., location in space). Such a condition would be an active attentional condition rather than the passive approach taken here.

A within-subject manipulation was used here to assess learning effects (trained vs. untrained frequency). This approach was taken to minimize impacts of procedural learning that can mask perceptual learning when using untrained control subjects [42]. However, because of this, we also cannot determine whether there was any generalization from the trained to untrained frequency. We expect that the effects seen here would be even stronger when using an untrained control group for comparison.

5. Conclusions

That differences were observed between trained and untrained frequency tones in EEG responses during passive presentation suggests that selective attention is not the only process involved in auditory detection learning. Auditory detection learning likely relies on both long-term representation-based changes *and* attentional biases. Future work aimed at testing predictions of theory and potential application will benefit from considering both processes.

CRediT authorship contribution statement

Matthew G. Wisniewski: Conceptualization, Methodology, Software, Formal analysis, Writing - original draft, Visualization. **Natalie J. Ball:** Conceptualization, Formal analysis, Investigation, Writing - original draft, Funding acquisition. **Alexandria C. Zakrzewski:** Conceptualization, Methodology, Investigation, Writing - review & editing, Supervision. **Nandini Iyer:** Conceptualization, Writing - review & editing, Funding acquisition. **Eric R. Thompson:** Conceptualization, Writing - review & editing. **Nathan Spencer:** Conceptualization, Writing - review & editing.

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