Neural Responses and Perceptual Sensitivity to Sound Depend on Sound-Level Statistics

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Abstract

Adaptation to sound-level statistics is thought to be crucial for optimal perception, but research has focused on neurophysiological recordings, mostly in non-human mammals. Behavioral evidence for adaptation to sound-level statistics is sparse. Here we use electroencephalography (EEG) and behavioral methods to investigate how the statistics of sound-level distributions affect neural activity in auditory cortex and the detection of near-threshold changes in sound amplitude. We presented noise bursts with sound levels drawn from distributions with either a low (15 dB SL) or a high (45 dB SL) modal sound level. One group of participants listened passively to the stimulation while EEG was recorded (Experiment I). A second participant group performed a behavioral amplitude-modulation detection task (Experiment II). Neural responses to noise bursts and sensitivity to amplitude modulation depended on sound-level statistical context: Consistent with an account positing that the sensitivity of neurons to sound intensity changes with ambient sound level, neural responses and amplitude-modulation sensitivity (d') for noise bursts at moderate intensities were larger for low ambient sound levels compared to high ambient sound levels. Neural activity appears to adapt to sound-level statistics in humans, perhaps fine-tuning perceptual sensitivity to optimize detection of subtle changes in sound amplitude.

Keywords: Stimulus statistics, adaptation, perceptual sensitivity, amplitude modulation, electroencephalography

Introduction

Acoustic environments are highly variable. In the course of a day, someone may work in a library, commute by subway, listen to a podcast, and attend a stadium concert. How does that person manage to hear effectively in all those different environments? Some perceptual flexibility is crucial for the optimization of perception and behavior[1-4]. However, neurons that support audition are limited in the range of sensory stimulation to which they respond[5,6]. For example, spiking activity of auditory nerve fibers in rodents sensitively discriminates between different sound levels over a limited range, typically between 10 and 40 decibels[7,8]. Sound levels outside this range either saturate neural responding (i.e., when sounds are more intense than the upper response limit) or do not elicit a response (i.e., when sounds are less intense than the lower response limit; Figure 1). Humans can perceptually identify small differences in the levels of two sounds over a 120-decibels range, even though individual neurons only respond over a ~40 dB range[6,9].

Achieving a wide perceptual range with a limited neuronal range is thought to be accomplished by a dynamic adjustment of the response range (input-output function) of neurons to sound-level statistics in the environment (Figure 1A)[10,11]. This process – called adaptation to stimulus statistics, dynamic range adaptation, or gain control[1,12-16] – involves shifting the response range of neurons depending on the mean or modal sound level in an acoustic environment[10,11,17-22]. When ambient sound levels are low, neurons are more sensitive and more responsive, but saturate for moderate- to high-level sounds, compared to when ambient sound levels are moderate to high (red and teal lines in Figure 1A, respectively). The red and teal dots in Figure 1A indicate predicted responses to target stimuli of lower or moderate intensity, presented in the two different sound contexts (low ambient level; high ambient level). If adaptation shifts the neural response range based on sound-level statistical context as hypothesized, we should observe a large effect of context on a moderate-level target sound, and much less effect of context on a lower level sound (Figure 1).

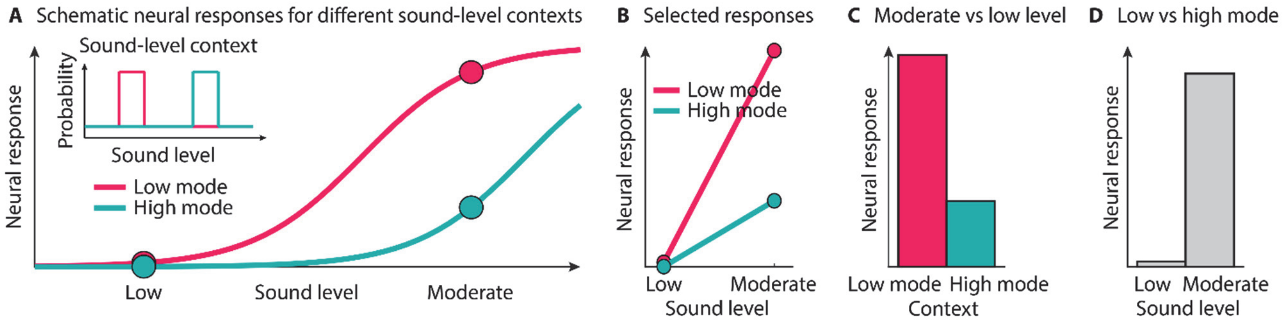

Figure 1: Schematic depiction of neural adaptation to sound-level statistics. Adopted from empirical data[10,11,21]. A: Predicted neural responses as a function of sound level for two sound-level contexts with different modal sound levels (low vs. high; inset). Dots mark two target-sound levels (low and moderate intensity), similar to the neural and behavioral analysis of empirical data (Experiment I and II). The inset schematically depicts the probability with which sound levels occur in the two contexts. B: Same response data as in A, but focusing only on the low and moderate target-sound levels (dots in panel A). C: Response range (i.e., subtraction of responses to less intense sounds from responses to moderately intense sounds) for the two contexts (low vs. high mode). D: Response difference between the low-mode and high-mode statistical contexts, separately for less and moderately intense sound levels.

Most research on adaptation of neural activity to sound-level statistics has been conducted using neurophysiological techniques in non-human mammals[10,11,13,17-20,23]. We have recently demonstrated using magnetoencephalography that neural activity in human auditory cortex adapts to sound-level statistics (i.e., to the modal sound-level)[21]. However, whether such adaptive changes confer benefit to perceptual sensitivity is less clear. We expect that the ability to perceive changes in sound level, such as those introduced by amplitude modulation, will also be affected by sound-level context (e.g., low vs. high mode), in a way that reflects the neurophysiological data – i.e., better sensitivity for moderate target sounds than low-level target sounds, uniquely in the context with a low modal level.

In a behavioral study, Simpson and colleagues[24] assessed whether relative loudness perception depends on the modal sound level of the auditory context. Participants were presented with sound pairs whose sound levels were drawn from a distribution with either a low or a high modal level, and they indicated which of the two sounds was louder. Discrimination performance was sensitive to the context's modal level. However, inconsistent with statistical adaptation measured neurophysiologically (Figure 1)[10,11,17,18,21], sound-level discrimination was better for low-intensity compared to higher-intensity target sounds in the high-modal context[24]. Neurophysiological work, in contrast, suggests that neurons are not very sensitive to low-intensity sounds when the ambient sound level is high (Figure 1A). The experimental paradigm used in this previous study[24] differed from that typically used to study neural adaptation to sound-level statistics[10,11,17,18,23]: the interval between sound pairs was substantially longer, compared to neurophysiological studies, to allow for a behavioral response[24]. It is not clear whether neural adaptation to sound-level statistics is effective over these longer intervals.

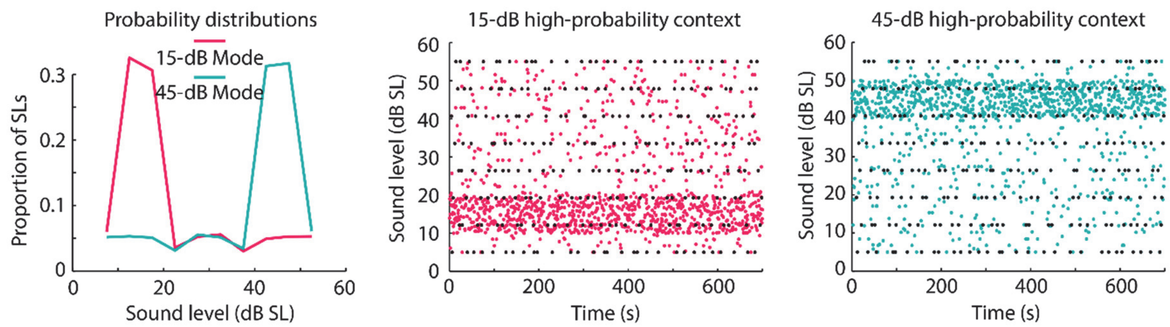

Figure 2: Experimental stimulation used in Experiment I and II. Left: Example probability distributions used for the acoustic stimulation for the two statistical contexts: one had a modal sound level of 15 dB SL, the other one had a modal sound level of 45 dB SL. Middle/right: 1400 white noises with different sound levels (y-axis) were presented at a rate of 0.5 s within a 700-s block (x-axis). Each dot reflects the sound level of one noise stimulus. Black dots indicate the stimuli of interest (targets) for which the effect of sound-level statistics on neural responses (Experiment I) and amplitude-modulation detection performance (Experiment II) was analyzed. For each target burst, its level and the level of the directly preceding noise burst were identical across contexts (15 dB SL and 45 dB SL modal level).

In the current study, we use a common stimulation paradigm to examine the effects of sound-level statistics on neural responses (Experiment I) and perceptual sensitivity to fluctuation in a sound's amplitude (Experiment II). Young adults listened to white-noise bursts (0.1 s duration; 0.5 s onset-to-onset interval) whose sound levels were drawn from a distribution with either a 15-dB or a 45-dB modal level (Figure 2). The main analyses focused on neural and behavioral responses to noise bursts (targets) for which the sound level, and the sound level of the directly preceding noise, were identical across the two statistical contexts (black dots in Figure 2, middle/right). This allowed us to investigate the effects of longer-term sound-level statistics on neural responses and perception[21].

Results

Experiment I: P1-N1 peak-to-peak amplitude depends on sound intensity and sound-level context

EEG was recorded from seventeen normal-hearing adults (18–31 years), while they listened to 0.1-s white-noise bursts presented in two sound-level contexts (Figure 2). Participants watched a muted, subtitled movie during the experiment. Sensitivity of neural responses to sound level was assessed by binning the responses to each sound (across both contexts) into five sound-level categories (10-dB width, centered on 10, 20, 30, 40, and 50 dB SL[21]). Single-trial responses within each category were averaged (Figure 3, left) and the P1-N1 peak-to-peak amplitude was calculated separately for each participant[25-27]. A linear function was fit to P1-N1 amplitude data as a function of the five sound levels independently for each participant. Slopes (linear coefficients) were reliably larger than zero ($t_{16} = 5.402$, $p = 5.8 \times 10^{-5}$, $r_e = 0.804$; Figure 3, right), demonstrating that the P1-N1 amplitude increased with increasing sound level[28-30].

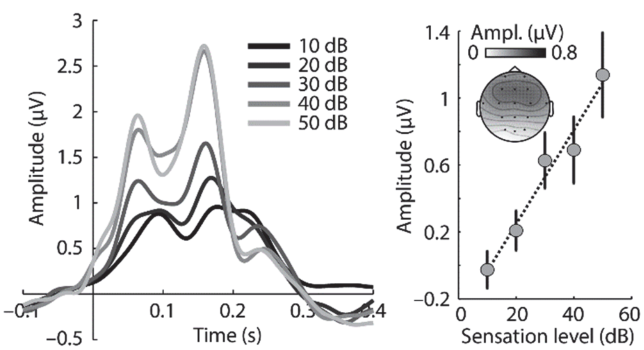

Figure 3: Overall response sensitivity to sound level (across sound-level contexts). Left: Response time courses for five different sound-level categories (averaged across a fronto-central electrode cluster). **Right:** P1-N1 peak-to-peak amplitude for each sound level (P1 and N1 were estimated for each participant separately). The dashed line reflects the averaged slope of the linear fit. Error bars reflect the standard error of the mean.

P1-N1 responses to noise bursts were compared between two different sound-level contexts presented in three blocks each: in one context, the modal level of the noise bursts was 15 dB, whereas it was 45 dB in the other context[21]. Critically, analyses focused on noise bursts for which the intensity, and the intensity of the directly preceding burst, were identical across contexts (these targets are indicated by black dots in Figure 2, middle/right). Hence, any difference in neural response between stimuli from the different distributions must be due to the longer-term sound-level statistical context.

In order to maximize the signal-to-noise ratio of the neural responses, responses to target bursts were binned according to target intensity, separately for the two statistical contexts: responses from targets with intensities below 30 dB SL were combined (mean of 15.7 dB SL), as were those with intensities higher than 30 dB SL (mean of 44.3 dB SL). The P1-N1 peak-to-peak amplitude was calculated for both contexts, for both target-intensity categories, separately for each participant (Figure 4A).

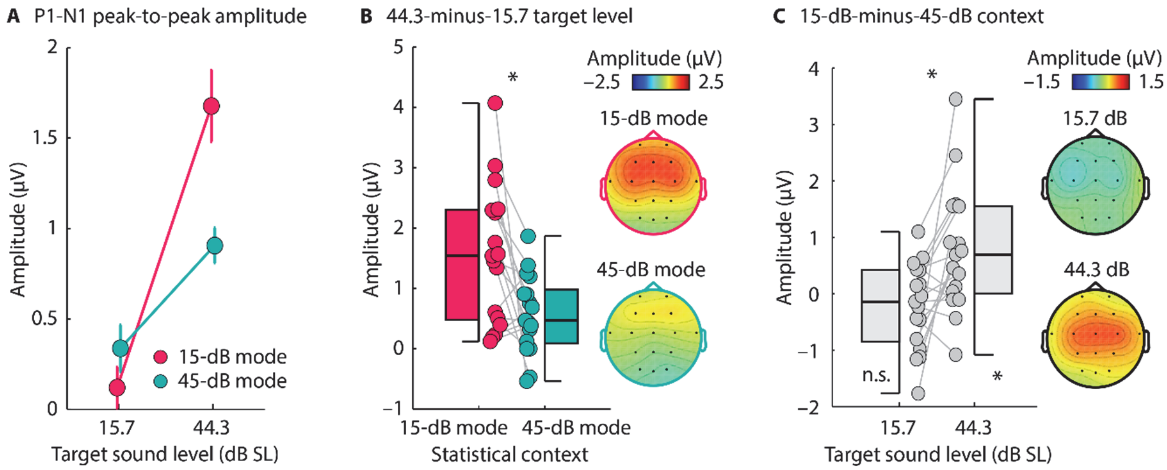

Figure 4: Neural responses to noise bursts in two different sound-level contexts. A: P1-N1 peak-to-peak amplitude for target-noise bursts with different intensities (one centered on 15.7 dB and one on 44.3 dB) for the 15-dB SL context and for the 45-dB SL context. Error bars reflect the standard error of the mean (removal of between-subject variance[31]). The interaction between context and target-intensity category is significant ($p < 0.05$; compare to predictions in Figure 1A,B). B: Response difference between target-intensity categories: results from subtracting the response amplitude for the 15.7 dB target-intensity category from that for the 44.3 dB target-intensity category, separately for the two sound-level contexts. As predicted, we see a smaller difference in the high-level context compared to the low-level context. Topographical distributions reflect the mean response difference between the two target-intensity categories, separately for the 15-dB context and the 45-dB context. C: The same interaction shown the other way: Amplitude difference between the 15-dB SL and 45-dB SL contexts, separately for low- and high-intensity targets. A positive value means a larger amplitude for the 15-dB SL compared to the 45-dB SL context. Topographical distributions reflect the mean response difference between the two statistical contexts. *$p \leq 0.05$, n.s. – not significant

A repeated-measures analysis of variance (rmANOVA) revealed that P1-N1 amplitudes increased from the low to high Target-Intensity Category (main effect: $F_{1,16} = 44.925$, $p = 5.1\times10^{-6}$, $\eta^2_p = 0.737$). The main effect of Context was not significant ($F_{1,16} = 2.778$, $p = 0.115$, $\eta^2_p = 0.148$), but the Context × Target-Intensity Category interaction was ($F_{1,16} = 9.599$, $p = 0.0069$, $\eta^2_p = 0.375$). The P1-N1 amplitude difference between targets categorized as high-intensity (44.3-dB category) and low-intensity (15.7-dB category) was larger in the low-intensity context (15 dB SL context) compared to the high-intensity context (45 dB SL context; Figure 4B), as predicted (see Figure 1C). Looking at the same interaction the other way, the effect of context was larger when target sounds were of higher intensity (44.3-dB category) than when they were less intense (15.7-dB category; Figure 4C), as predicted; see Figure 1A. The effect of context on responses was significant for the higher-intensity (44.3 dB) target category ($t_{16} = 2.877$, $p = 0.0109$, $r_e = 0.584$), but not for the lower-intensity category ($t_{16} = -1.176$, $p = 0.257$, $r_e = 0.282$; Figure 4C). Topographical distributions suggest that auditory cortex underlies the observed neural responses (Figure 4B, C)[32,33].

In sum, the results of Experiment I show that P1-N1 responses generated in auditory cortex, depend both on the target intensity and on the longer-term distribution of intensities (context). The results are consistent with recent work in humans using sine tones[21] and with previous work in animals[10,11,17,18]. The data suggest that response sensitivity shifts dynamically with modal level, enhancing sensitivity to moderately intense sounds in environments with a low modal level (see Figure 1). In Experiment II, we used to same paradigm as in Experiment I in order to elucidate the perceptual consequences of such neural changes.

Experiment II: Perceptual sensitivity to AM depends on sound-level context

The effect of sound-level statistics (context) on perceptual sensitivity was investigated by applying amplitude modulation (AM; 50 Hz) to the target sounds of Experiment I and comparing detection performance across contexts, as in Experiment I (non-target, filler, noise bursts were unmodulated). An AM-detection task was chosen because AMs are fluctuations in sound level, and neural adaptation to sound-level statistics is hypothesized to affect sound level acuity.

In order to equate the difficulty of AM detection across the target-sound levels, six participants (20–27 years) who did not participate in Experiment I or II participated in a pre-test to estimate the function (linear slope) that relates AM detection thresholds to target-sound levels. This function was then applied to the AM detection threshold that was estimated for one sound level (40 dB SL) for each participant of Experiment II (N =22; aged 18-31 years; all participants were naive), in order to determine the AM depth that yields 75% detected targets for each of the eight target intensity levels of the experimental protocol depicted in Figure 2 (see Experiment II pre-test methods and Figure 5, for details).

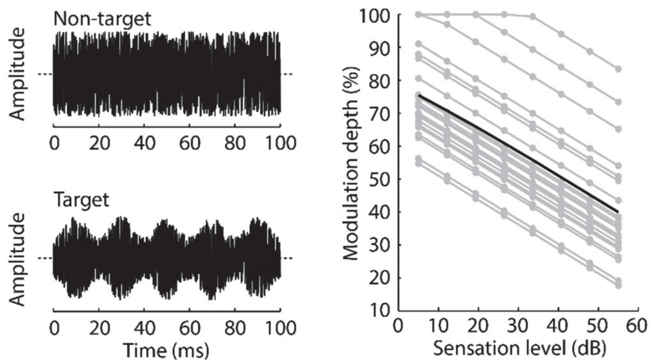

Figure 5: Acoustic stimuli and AM depths for behavioral Experiment II. Left: Example waveforms of non-target (filler, unmodulated) and target (50-Hz amplitude-modulated) noise bursts used in Experiment II. In the example, the amplitude of the target noise burst is modulated with a modulation depth of 50%. **Right:** AM depths used for each participant (gray lines) and sound level (gray dots) in Experiment II. The black line reflects the mean across participants. The slope common to all lines was calculated from the Experiment II pre-test. The height of each participant's line is determined by the AM depth yielding 75% correct detection in 40 dB SL noise bursts during preliminary testing.

As in Experiment I, responses to targets were binned according to target intensity, separately for the two contexts: responses from targets with an intensity below 30 dB SL (mean of 15.7 dB SL) were combined, as were those with an intensity higher than 30 dB SL (mean of 44.3 dB SL). Perceptual sensitivity (d') was calculated for both target-intensity categories and for both statistical contexts (Figure 6A), for each participant.

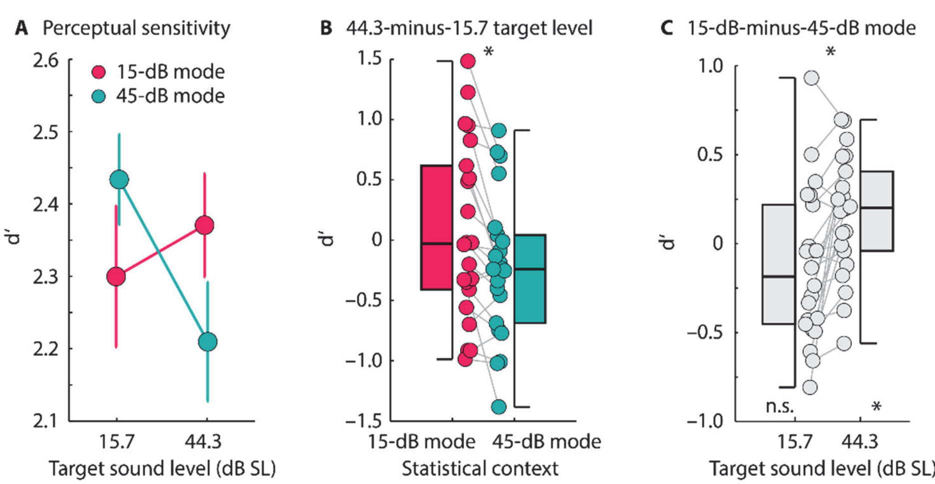

Figure 6: Perceptual sensitivity (d') for detecting amplitude-modulated target noises in two sound-level contexts. A: d' for detecting amplitude-modulated target bursts for different target-intensity categories (one centered on 15.7 dB SL and one on 44.3 dB SL) for the 15-dB SL and the 45-dB SL contexts; compare with Figure 1A,B. Error bars reflect the standard error of the mean (removal of between-subject variance[31]). The interaction is significant ($p < 0.05$). **B:** Difference in perceptual sensitivity between target-intensity categories: result from subtracting d' for less intense compared

to more intense targets for the 15-dB SL and the 45-dB SL context; compared with Figure 1C. C: The same interaction shown the other way: difference in d' between the 15-dB SL and 45-dB SL contexts, separately for low- and high-intensity targets. A positive value means a larger d' for the 15-dB SL compared to the 45-dB SL context. *p ≤ 0.05, n.s. – not significant

Performance on the task was good, with all conditions exceeding a mean d' value of 2. An rmANOVA indicated that the two factors Context and Target-Intensity Category exhibited a significant interaction ($F_{1,21}$ = 14.762, p = 9.5×10^{-4}, η^2_p = 0.413; Figure 6A). The difference in d' between low-intensity and high-intensity targets was larger in the low-level context (mode of 15 dB SL) compared to the high-level context (mode of 45 dB SL; Figure 6B). Comparing d' values between the two contexts, separately for each target-intensity category (low-intensity targets centered on 15.7 dB SL; high-intensity targets centered on 44.3 dB SL) revealed higher perceptual sensitivity to AM in the 15-dB context compared to the 45-dB context for high-intensity targets (t_{21} = 2.254, p = 0.035, r_e = 0.441), but not for low-intensity targets (t_{21} = –1.475, p = 0.155, r_e = 0.306; Figure 6C).

There was no effect of Context ($F_{1,21}$ = 0.035, p = 0.853, η^2_p = 0.002) nor an effect of Target-Intensity Category ($F_{1,21}$ = 0.319, p = 0.578, η^2_p = 0.015). The latter was expected because we normalized the AM depth for individual target-sound levels based on the Experiment II pre-test (Figure 5) to achieve equal task difficulty (i.e., AM-detection performance) for each target-sound level.

In sum, the results of Experiment II show that the detection of amplitude fluctuations (AM) in sounds is affected by sound-level statistical contexts. As predicted, sensitivity was enhanced for AM on higher-intensity targets compared to lower-intensity targets, uniquely when the ambient noise level was low. The statistical results of Experiment II resemble the dependency of neural data on statistical context demonstrated in Experiment I, and in other work on neural adaptation to sound-level statistics[10,11,17,18,21].

Discussion

The current study investigated the effects of sound-level statistical context on neural activity and perceptual acuity for sound level. Sound-level statistics were manipulated by presenting white noises at levels drawn from one of two distributions with different modes (15 dB vs. 45 dB). We observed that neural responses in auditory cortex and perceptual sensitivity to amplitude modulation were affected by the statistical sound-level context in a similar way.

In Experiment I, the P1-N1 amplitude was sensitive to target intensity and to sound-level statistics. The effect of target intensity (less intense vs. more intense level) on responses was greater for white-noise bursts presented in the context with a low modal sound level (15 dB SL) compared to the context with a high modal sound level (45 dB SL; Figure 4). These data are consistent with the hypothesis that neurons in the auditory system adjust their sensitivity by shifting the dynamic response range depending on the modal sound level in an acoustic environment (schematically depicted in Figure 1)[10,11,17,18,21]. We show more sensitivity and responding when the ambient context has a low modal level, compared to a higher modal level, particularly for moderately intense targets. Here we used white-noise bursts, unlike in our previous work, in which we used pure tones[21]. White-noise bursts activate the full extent of the cochlear partition and associated auditory nerve fibers – this avoids the issue that pure tones with more intense levels recruit more off-frequency (i.e., non-best frequency) fibers, which, in turn, may contribute to effects of sound-level context using pure tones.

Neural adaptation to sound-level statistics has been observed at different stages along the auditory hierarchy, including the auditory nerve[18,19], inferior colliculus[10,11,20,23], and auditory cortex[34]. Until recently, investigations of adaptation to sound-level statistics were limited to animal models. The current data, together with recent magnetoencephalography data[21], demonstrate response patterns that are consistent with adaptation to sound-level statistics in human auditory cortex. The mechanisms underlying statistical adaptation are not fully understood, but research in animals suggests that neural inhibition is likely an important contributor[4,17,35-38].

In Experiment II, we utilized the experimental paradigm (Figure 2) used to demonstrate that sound-level context influences neural responses to investigate effects on perception of amplitude modulation in sound. We observed that the difference in AM sensitivity between moderate-level targets (44.3 dB) compared to lower-level targets (15.7 dB) was larger in the context with a low modal sound level (15 dB SL) compared to the context with a high modal sound level (45 dB SL; Figure 6). The behavioral effect of sound-level context resembled the effect of context on the EEG-recoded neural responses (Experiment I; Figure 4). Note that, in contrast to our neural data, there was no effect of target-intensity category on perceptual sensitivity (d'), because AM depth was normalized across target-sound levels to achieve equal AM-detection difficulty at different target levels. The effect of sound-level context on perceptual sensitivity is consistent with the hypothesis that neural adaptation to sound-level statistics optimizes perception[13,39].

In the current study, noise bursts were presented every 0.5 seconds (with a 0.4-s silent interval), and targets were identical between contexts as were the noise bursts preceding the targets. Thus, 0.9 s would have elapsed between the end of the last filler (which could differ systematically between contexts) and the onset of the measured target. This is too long an interval for masking to be operating[40,41,42], or for any other simple explanation of the effect. The differences in the effect of target intensity on AM-detection sensitivity must be due to the longer-term sound-level statistics, likely over multiple seconds[15].

Recent data suggest that aging and hearing loss impair neural adaptation to sound-level statistics[21,23]. Neurons in the inferior colliculus of noise-exposed animals[23] and neurons in auditory cortex of older human adults[21] remained sensitive to sound level under conditions leading to fully adapted neural responses in control animals and younger adults, respectively. These changes related to hearing impairment have been proposed to underlie, at least in part, the established difficulty that older people have with filtering out irrelevant sound information[21,23]. A demonstration that sound-level statistical context differentially affect perception in people with hearing impairment, compared to normal-hearing controls, still awaits future studies.

We investigated how sound-level statistics affect neural adaptation and perception by utilizing a paradigm in which white-noise bursts were presented in sound-level contexts with different modes (low and high). We show that neural response sensitivity to sound level and perceptual sensitivity to sound-level modulation are affected by sound-level contexts. The pattern of results is consistent with the hypothesis that neural responsiveness changes with the modal ambient sound level, such that neurons are more sensitive and more responsive when ambient sound levels are low compared to when ambient sound levels are moderate to high (schematically depicted in Figure 1). The data indicate that the auditory system uses statistical information about sound level to fine-tune perception dynamically.

Methods and Materials

Participants

Seventeen adults participated in Experiment I (median age: 20 years; range: 18–31 years), six adults participated in the Experiment II pre-test (median age: 23 years; range: 20–27 years), and twenty-two adults participated in Experiment II (median age: 21 years; range: 18–31 years). Two additional participants were recorded for Experiment I, but the data were excluded because no neural N1 response could be identified even in blocks in which responses were non-adapted. One additional participant was excluded from Experiment II, because the person did not complete all blocks.

Participants reported no neurological disease or hearing impairment. They gave written informed consent prior to the experiment and were paid $5 CAD per half hour for their participation. The study was conducted in accordance with the Declaration of Helsinki, the Canadian Tri-Council Policy Statement on Ethical Conduct for Research Involving Humans (TCPS2-2014), and approved by the local Nonmedical Research Ethics Board of the University of Western Ontario (protocol ID: 106570).

Acoustic stimulation

All experimental procedures were carried out in a single-walled sound-attenuating booth within a larger quiet testing room in the Western Interdisciplinary Research Building (Brain & Mind Institute, Western University). Sounds were presented via Sennheiser (HD 25-SP II) headphones and a Steinberg UR22 (Steinberg Media Technologies) external sound card. Stimulation was controlled by a PC or Laptop (Windows 7, 64 bit) running Psychtoolbox in MATLAB software (MathWorks, Inc.).

Estimation of sensation level

Before each experiment, the sensation level (SL) was determined for each participant for a white noise stimulus using a method-of-limits procedure that we have described in detail in previous work[43,44]. Sounds presented to participants during the experiments were presented relative to the estimated sensation level.

Stimulus design

The experimental paradigm closely mirrored our previous work[21]. Noise bursts were presented in two different types of stimulation blocks (contexts) that differed with respect to the sound-level distributions from which a noise burst's sound level was drawn: for one context the modal sound level was 15 dB SL, for the other it was 45 dB SL (Figure 2). In order to investigate the effects of sound-level statistics on neural responses and perception, we eliminated the confounding effects of different acoustics by ensuring that the bursts for which data were analyzed, as well as the immediately preceding burst were identical across contexts (i.e., 15 dB SL vs. 45 dB SL). Participants listened to six (Experiment I) or four (Experiment II) blocks, half of them with a 15-dB modal sound level, and the other half with a 45-dB modal sound level.

In each 700-second long block, 1400 white-noise bursts, each with a duration of 0.1 s, were presented. The onset-to-onset interval was kept constant at 0.5 s. In each block, eight sound levels ranging from 5 dB SL to 55 dB SL (step size: 7.143 dB SL) were each presented 30 times, yielding 240 target noises per block. These stimuli were identical across all blocks (black dots in Figure 2, middle/right). The 240 noise bursts immediately preceding each of these targets were also fixed, such that for each of the 30 presentations of one of the eight sound levels, the sound level of the preceding noise took on one of 30 sound levels (range: 5 dB SL to 55 dB SL; step size: 1.724 dB SL) without replacement. Thus, the same 240 experiment pairs were presented in each block. The sound levels for the remaining 920 filler-noise bursts were chosen randomly (range: 5 dB SL to 55 dB SL; step size: 0.1 dB SL) depending on the sound-level context (Figure 2). For half the blocks, sound levels were randomly chosen from a sound-level distribution with a 15-dB high-probability region (red dots in Figure 2, middle). For the other half of the blocks, sound levels were randomly chosen from a sound-level distribution with a 45-dB high-probability region (teal dots in Figure 2, right). High probability regions had a width of 10 dB centered on 15 dB SL or 45 dB SL (Figure 2, left). The experimental pairs and the fillers were randomly intermixed in each block and presented such that at least one filler occurred before and after each experimental pair. Sound-level context blocks alternated, and the starting sound-level context was counter-balanced across participants.

Analysis of the influence of sound-level context on neural responses (Experiment I) and perceptual sensitivity (Experiment II) focused on target bursts (i.e., the second noise burst in each experimental pair): these were identical across the two contexts (black dots in Figure 2, middle/right) as was the preceding noise burst.

In Experiment I, participants also listened to a seventh block of trials (the 'no-adaptation' block), in which white-noise bursts (0.1 s duration) were presented 40 times at an onset-to-onset interval of 10 s and a sound level of 55 dB SL. Neural populations were assumed to fully or almost fully recover from adaptation during the 10-s period between noise onsets[45-47], and the responses to these bursts were thus considered to reflect neural responding in a non-adapted state[21,48].

Experiment I: Effect of sound-level statistical context on neural responses

EEG recording and preprocessing

EEG signals were recorded at a 1024-Hz sampling rate from 16 electrodes (Ag/Ag–Cl-electrodes; 10-20 placement) and additionally from the left and right mastoids (BioSemi, Amsterdam, The Netherlands; 208 Hz low-pass filter). Electrodes were referenced to a monopolar reference feedback loop connecting a driven passive sensor and a common-mode active sensor, both located posterior on the scalp.

Offline data analysis was carried out using MATLAB software. Line noise (60 Hz) was suppressed in the raw data using an elliptic filter. Data were re-referenced to the average mastoids, high-pass filtered at a cutoff of 0.7 Hz (2449 points, Hann window), and low-pass filtered at a cutoff of 22 Hz (211 points, Kaiser window). Independent components analysis (runica method[49]; logistic infomax algorithm[50]; Fieldtrip implementation[51]) was used to identify and suppress activity related to blinks and horizontal eye movements. Data were divided into epochs ranging from –0.1 to 0.4 s (time-locked to burst onset). Epochs that exceeded a signal change of more than 180 µV for any electrode were excluded from analyses. All epochs were baseline-corrected by subtracting the mean signal in the 0.1 s prior to the noise-burst onset from each time point of the epoch (separately for each channel).

Data analysis

P1-N1 peak-to-peak amplitude. Data analysis focused on the P1-N1 peak-to-peak amplitude, as in previous work[25-27]. Response latencies can only be estimated accurately for responses with a sufficiently large amplitude. P1 amplitudes increase with increasing sound presentation rate[21,52], and the P1 peak latency was thus estimated from the responses to noise bursts in the statistical context blocks (mean across trials with sound levels >40 dB SL). In subsequent analyses, amplitude data centered on this estimate of the P1 latency were extracted. The N1 amplitude, in contrast, decreases with increasing presentation rate (assumed to reflect adaptation)[47,53]. The N1 peak latency was therefore estimated from the 'no-adaptation' block in which noise bursts were presented every 10 seconds and used to extract N1 amplitude data in context blocks. In order to calculate the P1-N1 amplitude in subsequent analyses, we subtracted the mean signal from the 0.01-s time window centered on the individually estimated N1 latency from the mean signal from the 0.01-s time window centered on the individually estimated P1 latency.

Response sensitivity to sound level. In order to investigate how sound level affects response amplitude (across statistical contexts), trials from all context blocks were sorted into one of five categories according to their sound level; these were 5–15, 15–25, 25–35, 35–45, 45–55 dB SL. Single-trial response time courses were averaged separately for each sound-level category. For each participant, the P1-N1 amplitude difference was extracted from the averaged time courses, separately for each sound-level category. In order to investigate whether responses increased with increasing sound level, a linear function was fit to the P1-N1 amplitude as a function of sound level. The slope of the linear function indicates the degree of response sensitivity to sound level. Each participant's data yielded one slope value: we tested whether the slopes differed from zero using a one-sample t-test.

Context-dependent response sensitivity. For this analysis, only responses to target bursts with the 8 different critical sound levels were analyzed (black dots in Figure 2). The number of trials at each of the 8 sound levels in the two contexts was relatively low (90 trials) and the response magnitudes were relatively small due to strong neural adaptation. In order to increase the number of trials in the response average, thereby increasing the signal-to-noise ratio, we binned the target responses into two categories based on target sound levels (separately for the two contexts). After baseline correction, single-trial time courses for noise bursts with a level below 30 dB SL (i.e., four levels between 5 and 26.4 dB with a mean of 15.7 dB SL) were averaged as were the time courses for bursts with a level above 30 dB SL (i.e., four levels between 33.6 and 55 dB with a mean of 44.3 dB SL). P1-N1 response magnitudes were analyzed using a repeated-measures ANOVA with the factors Context (15 dB SL, 45 dB SL) and Target-Intensity Category (2 levels, centered on 15.7 and 44.3 dB SL).

Experiment II pre-test: Determination of AM-detection thresholds at different sound levels

A psychophysical pretest was conducted using the method of constant stimuli, in order to estimate the AM depth corresponding to the detection threshold for a 50-Hz AM in a 0.1-s duration white-noise burst, for different sound levels. The slope of the function relating intensity to AM-detection sensitivity was then used in Experiment II (Figure 5).

White-noise bursts (0.1 s duration) were presented every 0.5 s. Targets bursts were amplitude modulated at a rate of 50 Hz; fillers were unmodulated. Participants listened to three blocks of noise bursts, each containing 160 targets and 906 fillers. Participants were instructed to press a button on a keyboard as soon as they detected a target. Each target was presented at one of four sound levels (i.e., 15, 25, 35, or 45 dB SL) and one of eight AM depths (from 2% to 100%, in steps of 14%). In each block, five targets were presented at each sound-level and AM-depth combination. The sound levels for fillers were randomly drawn from a uniform distribution ranging from 5 dB SL to 55 dB SL. Between three and eight fillers were interposed between successive targets. Participants performed one to three brief training blocks to familiarize them with the stimulation and task.

A target was considered detected if a key press was made between 0.1–1.1 after the target onset. The proportion of detected targets was calculated for each sound level and AM depth, pooled across all six participants. A logistic function was fit to the proportion of detected targets as a function AM depth, separately for the four different sound levels. For each sound level, the AM depth that yielded 50% detected targets was estimated from the fitted logistic function. In order to estimate the AM depth for any of the eight target-sound levels used in Experiment II (Figure 2), we fitted a linear function to the 50% thresholds as a function of the four pre-test target levels. The slope from the linear fit was used in Experiment II to relate AM depth to target-sound level.

Experiment II: Effect of sound-level statistical context on AM detection

The stimuli of Experiment II were identical to those in Experiment I, except that target bursts (see Figure 2; black dots) were amplitude modulated at 50 Hz while fillers remained unmodulated. Participants performed the AM-detection task, as in the Experiment II pre-test, for four stimulation blocks. Sound levels in the blocks were drawn from one of the two sound-level distributions (with a mode of 15 dB SL or 45 dB SL) as in Experiment I. Blocks alternated between the 15 dB SL context and the 45 dB SL context (counterbalanced across participants). As in Experiment I, the sound levels of targets, and the level of preceding bursts, were identical across contexts (Figure 2, black dots). Hence, any difference in AM-detection performance between contexts can be attributed to the sound-level statistics.

For Experiment II, we wished to equalize the AM-detection rate across target-sound levels in order to avoid differences in task difficulty for different target intensities. This involved estimating the AM depth that would yield 75% detected targets at one sound level (40 dB SL) in a pre-experiment block and calculating the AM depth for all target intensities relative to this 75%-AM depth using the estimated slope from the Experiment II pre-test that relates AM-detection thresholds to sound levels. In the pre-experiment block, ten 40-dB SL targets at each of eight modulation depths (2% to 100%, in steps of 14%) were presented among 450 fillers drawn from a uniform level distribution that ranged from 5 to 55 dB SL. The proportion of detected targets was calculated for each AM depth and a logistic function was fit to the data to obtain the AM depth that yielded a 75% detection rate at 40 dB SL. AM depths for all target intensities were then estimated from the slope of the Experiment II pre-test relative to the AM depth yielding the 75% detection rate at 40 dB SL. Note that the identical AM depths were used for targets in both statistical contexts during the main part of Experiment II, and any difference in AM-detection performance between contexts can thus be attributed to the sound-level statistics.

For the analysis of Experiment II data, a target was considered detected if a key press was made within 0.1–1.1 after the target onset. As in Experiment I, we binned targets into two categories based on burst intensity in order to increase the number of trials (and thus signal-to-noise ratio). Targets with a sound level below 30 dB SL (mean of 15.7 dB SL) were analyzed separately from those with a sound level above 30 dB SL (mean of 44.3 dB SL). For each participant, the proportion of detected targets was calculated separately for each sound-level context (15 dB SL, 45 dB SL), and each target-intensity category (15.7 dB, 44.3 dB). In order to calculate perceptual sensitivity (d'), the false alarm rate was calculated using a method applicable to paradigms with high event rates such as the current one[54]. Perceptual sensitivity (d') values were subjected to a repeated-measures ANOVA with the factors Context (15 dB SL, 45 dB SL) and Target-Intensity Category (15.7, 44.3 dB SL).

Effect sizes

Throughout the manuscript, effect sizes are provided as partial eta squared (η_p^2) for repeated-measures ANOVAs and as r_e ($r_{equivalent}$) for t-tests[55].

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Author contributions

BH, TA, ISJ designed the study. BH and TA programmed the experiments, recorded the data, and analyzed the data. BH and ISJ wrote the manuscript. All authors reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Data availability

The datasets generated during the current study are not publicly available because participant consent for public-data sharing was not obtained. Data are available from the corresponding author on reasonable request.

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