Sensitization to masked tones following notched-noise correlates with estimates of cochlear function using distortion product otoacoustic emissions

Xiang Zhou
Department of Biomedical Engineering, The City College of the City University of New York, Steinman Hall, Room T-401, Convent Avenue, 140th Street, New York, New York 10031

Simon Henin, Suzanne E. Thompson, and Glenis R. Long
Speech and Hearing Sciences, Graduate Center, City University of New York, 365 Fifth Avenue, New York, New York 10016

Lucas C. Parra[a)]
Department of Biomedical Engineering, The City College of the City University of New York, Steinman Hall, Room T-401, Convent Avenue, 140th Street, New York, New York 10031

(Received 17 September 2009; revised 23 November 2009; accepted 23 November 2009)

Neuronal gain adaptation has been proposed as the underlying mechanism leading to the perception of phantom sounds such as Zwicker tones and tinnitus. In this gain-adaptation theory, cochlear compression plays a significant role with weaker compression leading to stronger phantom percepts. The specific aim of this study was to find a link between the strength of neuronal gain adaptation and cochlear compression. Compression was assessed using distortion product otoacoustic emissions (DPOAEs). Gain adaptation is hypothesized to manifest itself in the sensitization observed for the detection of masked tones when preceded by notched noise. Perceptual thresholds for pure tones in notched noise were measured at multiple frequencies following various priming signals. The observed sensitization was larger than expected from the combined effect of the various maskers. However, there was no link between sensitization and compression. Instead, across subjects, stronger sensitization correlated with stronger DPOAEs evoked by low-level primaries. In addition, growth of DPOAEs correlated reliably with perceptual thresholds across frequencies within subjects. Together, the data suggest that short-term dynamic adaptation leading to perceptual sensitization is the result of an active process mediated by the outer hair cells, which are thought to modulate the gain of the cochlear amplifier via efferent feedback.
 [DOI: 10.1121/1.3277156]

PACS number(s): 43.64.Jb, 43.66.Dc [BLM] Pages: 970–976

I. BACKGROUND

The subjective sensation of sound in the absence of a real stimulus is referred to as a phantom percept. Tinnitus and the Zwicker tone are phantom percepts induced in some subjects at frequencies of reduced auditory stimulation. We argued previously that these phantom percepts result from central neuronal gain adaptation, which increases sensitivity to a point where background neuronal activity is perceived as a phantom sound (Parra and Pearlmutter, 2007). The corresponding computational model suggested a link between the strength of the perceived phantom sounds and the compression factor of cochlear dynamics. Indeed, this previous study found empirically that Tinnitus subjects, who as a group have been shown to have reduced compression (Janssen *et al.*, 1998), are significantly more likely to perceive the Zwicker tone.

The basilar membrane responds to sound in a nonlinear fashion, providing an intensity-dependent gain to incoming sounds (see Cooper *et al.*, 2008 and Neely and Kim, 2008 for a review). This adaptive amplification is thought to be mediated by the outer hair cells (OHCs), which are in the position to modify basilar membrane mechanics on a cycle-by-cycle basis and is often referred to as the cochlear amplifier (see Cooper *et al.*, 2008). At lower signal levels amplification is stronger than at high signal levels at which point the basilar membrane is believed to become purely passive. This results in a compressive non-linearity, which provides a reduction in the output range of the incoming sound and an increase in dynamic range required for proper transmission to the auditory nerve. Adaptive gains have also been documented for central auditory processing stages. For instance, Dean *et al.* (2005, 2008) showed that rate-response curves of neurons in the inferior colliculus adjust in thresholds (sensitivity) and slope (gain) to the auditory stimulus intensity on a time scale of 100 ms.

The specific aim of this study was to find a link between the strength of this central neuronal gain adaptation and the instantaneous cochlear compression. Cochlear compression was assessed with high frequency resolution using a newly

[a)]Author to whom correspondence should be addressed. Electronic mail: parra@ccny.cuny.edu

developed method for obtaining distortion product otoacoustic emissions (DPOAEs), which extracts the generator component of the DPOAE (Long *et al.*, 2008).

To measure gain adaptation we took an indirect approach. Initial preliminary experiments (not shown here) indicated that following a notched noise, the sensitivity to faint sounds in the notch region should be increased. In the extreme, we hypothesized that this increased sensitivity results in the perception of a tone even in the absence of a sound, a phantom percept known as the Zwicker tone. However, we did not find an increase in sensitivity for pure tones in quiet, but for tones that were simultaneously masked by notched noise—a phenomenon that had been observed previously (Carlyon, 1989; Strickland, 2004). The surprising observation is that the addition of a long-duration masker, or precursor, can improve detection thresholds of a stimulus as the stimulus is delayed from the onset of the masker. This phenomenon is referred to as overshoot (e.g., Zwicker, 1965). Viemeister and Bacon (1982) and Thibodeau (1991) reported a similar effect with the use of an adaptor stimulus on the enhancement of a masker in a forward masking paradigm. When a preceding adaptor stimulus lacked the spectral content of the masker, an increase in masking was observed. In this scenario the enhancement effect was attributed to an increase in gain at the masker frequencies resulting from an adaptation to suppression of the components contained in the adaptor stimulus. Here we hypothesize that this sensitization is the result of neuronal gain adaptation, which increases sensitivity in the missing frequency band of the notch. We therefore use this sensitization as a measure of neuronal gain adaptation. In order to measure this sensitization psychophysically, a paradigm is established here that measures perceptual thresholds of a simultaneously masked pure tone in the presence of a long-duration precursor stimulus.

Two experiments were conducted: Experiment I aimed to establish a link between compression and sensitization, and experiment II aimed to confirm that this sensitization is not just a result of a linear process. The results of these experiments suggest that the observed sensitization is the result of an active process mediated by outer hair cell function, but that cochlear compression by itself does not necessarily affect its strength. The experiments also revealed a reliable correlation of compression with perceptual thresholds across frequency.

II. METHODS

A. Subjects and procedures

Eighteen subjects were recruited for this study (11 for experiment I and 7 for experiment II, see below). Initial audiograms were performed to exclude cases of moderate and severe hearing loss. All but two subjects had hearing thresholds of less than 20 dB hearing level (HL) at all audiometric frequencies. Two subjects each had mild hearing losses of less than 30 dB HL at one single frequency. Subjects were between 20 and 45 years of age and were recruited from the main campus of the City University of New York. All subjects were paid $10 an hour for participating in the experiment. An Institutional Review Board consent form was signed before the experiment. The experiment consisted of a psychoacoustic task as well as DPOAE measurement. The total experiment time per subject was approximately 4 h.

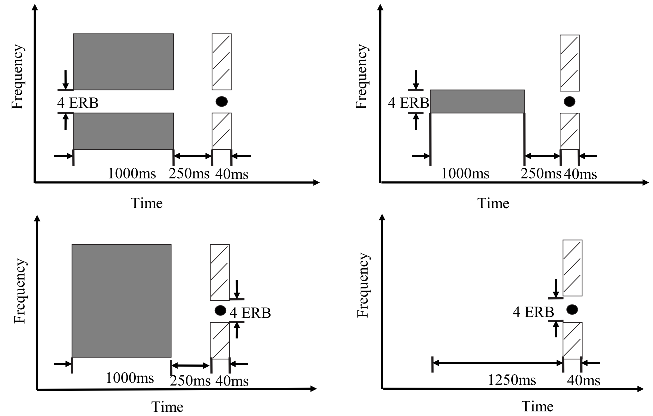

FIG. 1. Schematic of spectral content in psychoacoustic experiment. Thresholds were obtained for a brief probe tone (indicated by the black dot) simultaneously masked by notched noise (light shaded area). The four panels show the different precursors (dark shaded area) clockwise from the top left: notched-noise, bandpass-noise, no precursor/quiet, and white noise.

B. Psychoacoustics: Primed notched-noise masking

Masked-thresholds were measured using a three-interval three-alternative forced-choice (3I3AFC) paradigm with an adaptive threshold-tracking procedure. During the experiment subjects were seated in a Industrial Acoustics Company (IAC) sound-treated booth. For a given trial, the listener pressed one of three keys to indicate the interval in which the probe tone was perceived. A visual aid marked each interval and feedback was provided after each response to indicate if the response was correct or incorrect.

The stimulus contained the following three components, which are represented schematically in Fig. 1: (1) a 1000 ms precursor period which can have one of four precursors: notched noise, bandpass noise, white noise, or no precursor ("quiet"). The notched- and bandpass-noise precursors had a 4-ERB bandwidth and the noise was fixed at 50 dB sound pressure level (SPL) overall $[\mathrm{ERB}(f)=0.108f+24.7$ at center frequency $f]$; (2) a variable-level probe tone (initial level of 50 dB SPL), and (3) a fixed-level (50 dB SPL overall) simultaneous notched-noise masker (4-ERB notch width). In all conditions the total durations (including onset/offset ramps) of the precursor, masker, and signal were 1000, 40, and 40 ms, respectively. The probe tone and simultaneous notched-noise masker had 5 ms Hanning window onset and offset ramps. The precursor had 50 ms Hanning window ramps. There was a 250 ms time delay between the offset of the precursor and onset of the simultaneous notched-noise masker. All stimuli were generated digitally and played via an M-audio USB sound-card with 24-bit resolution at a sampling rate of 44.1 kHz. These stimuli were routed through a headphone buffer (TDT HB7) before being presented to the listeners via Sony headphones MDR-7506. All signals were filtered to equalize the spectrum of the specific pair of headphones. Equalization filters were obtained by recording a white noise signal emitted by the headphones with a calibrated microphone (Brüel & Kjær, Nærum Denmark, model 2218) inside a KEMAR head and torso simulator. Filter coefficients were computed from this using linear prediction coefficients of order 20. During each experiment, masked thresholds were measured at signal frequencies ranging from 1 to 4 kHz in steps of 250 Hz. Each trial consisted of three observation intervals. The primed precursor and simultaneous masker were presented in all three intervals, and the probe tone was randomly presented in one of three intervals. The threshold was measured using a modified version of the threshold-tracking procedure known as Parameter Estimation by Sequential Testing (PEST) (Taylor and Creelman, 1967), which estimated the threshold level at the 70% correct point on the psychometric function. In this procedure, the initial tone level was set to 50 dB SPL and decremented with a step size of 8 dB. After the first reversal the step size was reduced to 4 dB and after an additional reversal to 2 dB. The threshold estimate was taken as the mean of the last four reversals with a 2 dB step size. Data collection did not begin until a listener had several practice trials with the experimental paradigm. Presentation of a single frequency condition was randomized across subjects. Each threshold reported here represents the mean over two repetitions of this procedure. In experiment I the range of these two measures (max-min) pooled across frequencies and subjects was 2.7 dB SPL.

In the first experiment (experiment I), 11 subjects were tested in the bandpass- and notched-noise precursor conditions. Two threshold estimates were obtained for each condition and averaged to obtain the final threshold. One subject was excluded from the analysis because a second estimate could not be obtained. An additional seven subjects participated in a second experiment (experiment II) and were tested using all four precursor conditions (bandpass, notched, white, and quiet).

C. Distortion product otoacoustic emissions

DPOAE input-output functions were obtained from all subjects and were used to estimate basilar membrane response. There are several ways to estimate basilar membrane input/output (I/O) functions such as measuring a growth of masking (GOM) function or measuring temporal masking curves (TMCs) (e.g., Rosengard *et al.*, 2005). In this paper, DPOAEs provide an objective measure of cochlear compression. A technical challenge for DPOAEs is to ensure that one measures the response from just one frequency region in the cochlea. DPOAEs are generated in the cochlea in the region where two nearby primary tone stimuli maximally overlap (Shera, 2004). Once the DPOAE is generated, the signal travels both basally toward the oval window and also apically to its own characteristic place on the basilar membrane, where it generates an OAE similar to that generated by the external stimulus. The resulting components have the same frequency but originate from two different regions of the cochlea. To evaluate nonlinear growth, one must extract the component from the generator (maximum overlap) region alone (Mauermann and Kollmeier, 2004).

DPOAEs were obtained from one ear of each subject, who was seated in a recliner in a double-walled IAC sound-treated booth. Custom MAC software (OSX) was used to generate the primaries and to record the ear canal signals. Sweeps were presented via etymotic ER-10A earphones connected to the computer via a MOTU828 firewire interface (24 bit, 44.1 kHz). Ear canal signals were recorded with an Etymotic ER-10A microphone/preamplifier system and amplified by a Stanford SR560 low-noise amplifier connected to and controlled by the same computer. The stimuli used for DPOAE measurement were continuously sweeping primaries with a fixed primary ratio (f_2/f_1) of 1.22, as described by Long *et al.* (2008). Primary frequencies f_1 and f_2 ($f_1 < f_2$) were logarithmically swept from an f_2 frequency of 1000–4000 Hz at a rate of 2 s/octave. Primary tone presentation levels were set based on the scissors level paradigm (Kummer *et al.*, 1998) according to the equation $L_1 = \max(0.4L_2 + 39\ \text{dB SPL}, L_2)$. DPOAE levels were measured as a function of input signal level ($L_2 = 25-75$ dB SPL, 5 dB step).

Several sweeps were obtained for each primary level and averaged to increase the signal-to-noise ratio between the measured DPOAEs and the background noise. The number of sweeps obtained for each level depended on the primary level, with the lowest presentation levels requiring more sweeps ($L_2=25$, $N=60$) than the highest presentation levels ($L_2=75$, $N=12$).

Spectrograms of the individual sweeps were visually inspected, and noisy sweeps were eliminated before averaging at each level. A least-squares fit (LSF) procedure was used to extract the level of the DPOAE generator component for each averaged sound file using overlapping analysis windows of 1/2 s and a step size of 1/80 s (see Long *et al.*, 2008 for a review of the LSF procedure), resulting in an estimate of the magnitude and phase of the generator component of the DPOAEs.

III. RESULTS

The goal of the first experiment was to establish a link between cochlear compression and threshold sensitization. DPOAEs were obtained at various primary levels (25–75 dB SPL in steps of 5 dB) and perceptual thresholds for pure tones masked by notched-noise preceded by one of two precursors (bandpass or notched noise, see Fig. 1). Figure 2 shows the resulting data for one of the ten subjects that participated in this experiment. The top panel of Fig. 2 shows the DPOAE level in the range from 1 to 4 kHz. The bottom panel shows the perceptual thresholds obtained at 12 frequencies within that same range.

One measure of compression can be obtained by measuring the slope of DPOAE level growth as a function of the L_2 level (input/output slope). Low slope values correspond to a more compressive growth function and hence stronger cochlear amplification. In this instance, a compression factor was determined for each frequency as the difference in DPOAE levels between the highest and lowest input L_2 levels (75 and 25 dB SPL)—essentially the spread of the DPOAE curves—divided by 50 dB to obtain an input-output slope. Generally, for various subjects, these compression fac-

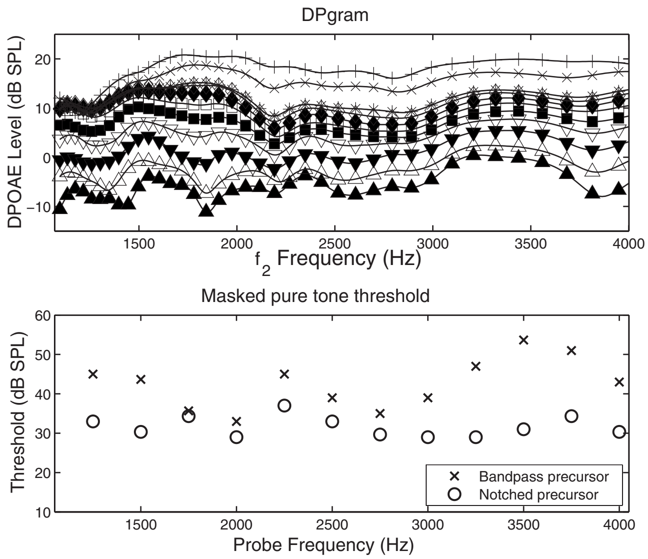

FIG. 2. Example of measured DPOAE and perceptual thresholds for one subject. Top: Each curve shows DPOAEs for one of 11 primary levels (25–75 dB SPL). A larger spread between levels indicates weaker compression. Bottom: Perceptual thresholds for tones under simultaneous notched-noise masking measured with two different precursor conditions (notched and bandpass noises). Distance between the data from two conditions indicates perceptual sensitization (L_2 primary levels: ▲: 25, △: 30, ▼: 35, ▽: 40, ■: 45, □: 50, ♦: 55, ◇: 60, *: 65, *x*: 70, and +: 75).

tors were within 0.25 and 0.5, indicating normal hearing (see Fig. 4). Compression factors above 0.5 coincided with mild hearing loss in two subjects (e.g., subjects 1 and 9). These values are in agreement with previous literature (Williams and Bacon, 2005). In addition to slope, we evaluated the mean DPOAE level as the average across all input L_2 levels (mean over all curves in Fig. 2, top).

Estimation of sensitization is based on the difference between perceptual thresholds with the notched- and bandpass-noise precursors. Preliminary unpublished experiments with no precursor established that thresholds are reduced by 5 ± 2 dB ($p<0.0001$, $N=4$) when the masked tone is preceded by a 3 s notched noise. For the present experiment, with a 1 s precursor duration, thresholds are reduced by 5.5 ± 1.1 dB ($p<0.0001$, $N=10$) when compared to the bandpass-noise condition. (The relationship between the no-precursor and bandpass-noise precursor conditions will be analyzed below.) These results are consistent with previously reported results using similar stimuli and precursor durations (Carlyon, 1989; Strickland, 2004).

Various psychoacoustic and DPOAE data were compared across frequency. Figure 3 shows these comparisons for subject 2. The heading of each panel gives the correlation coefficient (and the corresponding *p*-value) across frequency for each pair of measures. We found that elevated thresholds in the notched-noise condition were significantly correlated with reduced compression for eight of ten subjects (average correlation coefficient $c=0.67$ for subjects with $p<0.05$; Fig. 4). As a group, this correlation is highly significant, as shown in Fig. 5, top panel. Additionally, as a group, a significant correlation between compression and masked thresholds following the bandpass-noise precursor was found ($p<0.01$; Fig. 5, middle panel). However, the correlation between sensitization and compression was not significant. In-

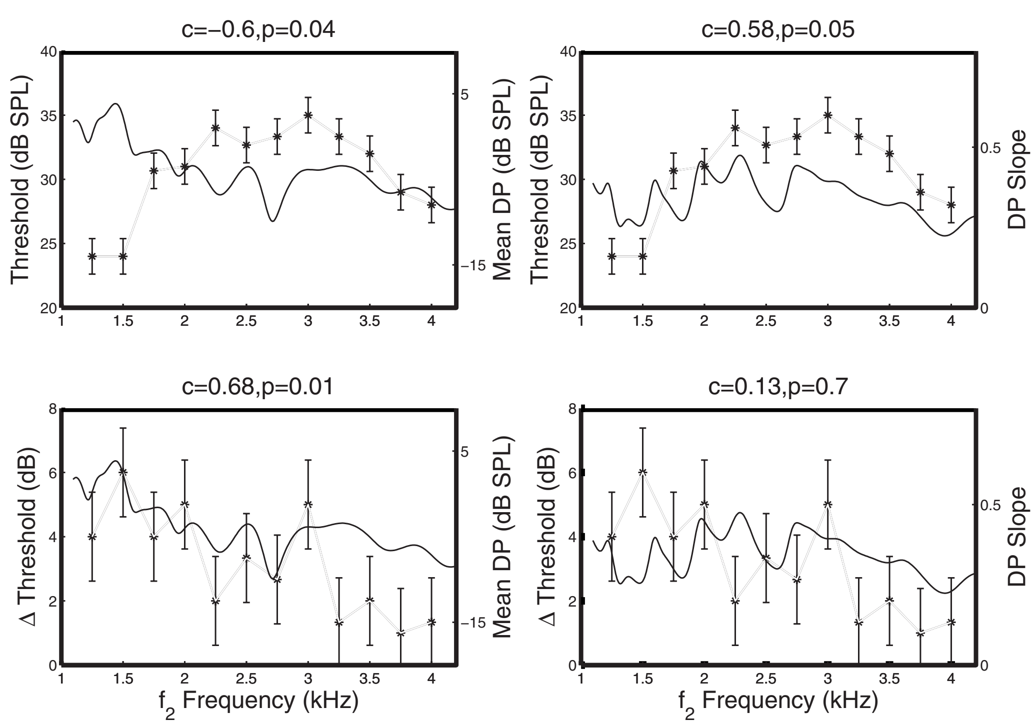

FIG. 3. Within-subject comparison of DPOAEs and psychoacoustic threshold measures. Top left panel plots correlation between masked threshold and mean DPOAE level (averaged across all L_2 levels) as a function of frequency. The top right panel shows the correlation between the threshold and compression (DPOAE I/O slope) as a function of frequency. The lower left panel shows the correlation between △Threshold (the difference between notched- and bandpass-noise thresholds) and the mean DPOAE level. The lower right panel shows the correlation between △Threshold and DPOAE compression (symbols represent psychoacoustic results, solid curve represents DPOAE measures, and error bars indicate range of two repeated measures pooled over frequencies).

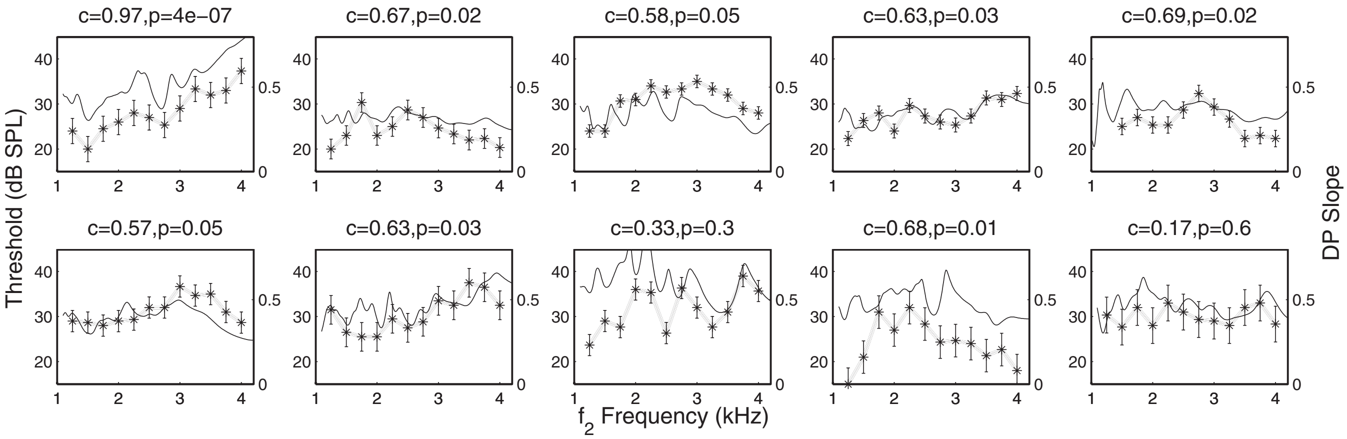

FIG. 4. Within-subject correlation of compression and masked thresholds. Panels show masked thresholds for each subject with notched precursor (symbols) and estimates of DP compression (solid curve). Error bars indicate range of two repeated measures pooled over frequencies. Significant correlations across frequency ($p<0.05$) were observed for eight of the ten subjects. For these subjects, $c=0.67\pm0.04$.

stead, stronger sensitization correlated with stronger DPOAEs for the lowest primary level measured ($c=0.24$, $p=0.008$, $N=10$, Fig. 5, bottom panel).

The sensitization of masked thresholds 250 ms after a notched-noise precursor is interpreted here as the result of neuronal gain adaptation (see Sec. IV for more details).

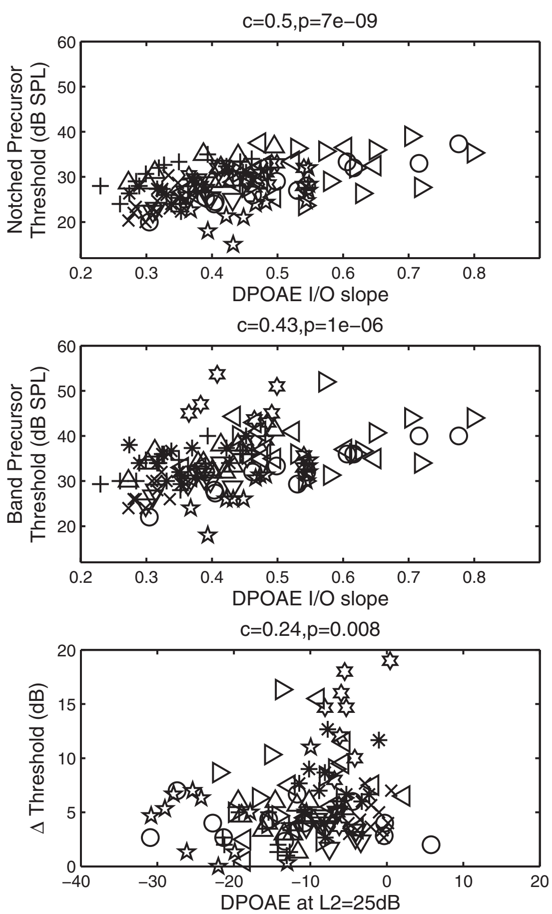

FIG. 5. Comparison of DPOAEs and masked thresholds for all subjects and all frequencies. The top panel shows the correlation between masked thresholds with notched-noise and estimates of compression for all ten subjects. The middle panel shows that thresholds with the bandpass-noise precursor correlate with estimates of compression. The bottom panel shows the correlation for DPOAEs obtained at the lowest primary level and sensitization (bandpass precursor-notched precursor).

To further quantify this sensitization and assess the differential effects of the on- and off-frequency bands in the precursor, an additional two precursor conditions were tested, namely, a quiet and a white noise condition. The top panel of Fig. 6 shows the results obtained in all four precursor conditions. Indeed these data confirm the preliminary observation that the notched-noise precursor significantly improves detection thresholds as compared to the quiet condition [two-way analysis of variance (ANOVA) with frequency and condition as factor, $p=0.004$, $N=7$, df=1, and $F=21.0$]. On average the improvement was 3.2 dB.

Can this improvement be explained as the effect of the off-frequency bands alone or does the contrast in the notched-noise precursor matter? The white noise condition has the same off-frequency power as the notched-noise condition, but also contains power in the on-frequency band. Therefore, its effect was compared to the combined effect of the notched- and bandpass-noise precursors by examining whether the threshold under the notched- and bandpass-noise conditions, I_N+I_B, was equivalent to the thresholds obtained in the white-noise and quiet conditions, I_W+I_Q. In other

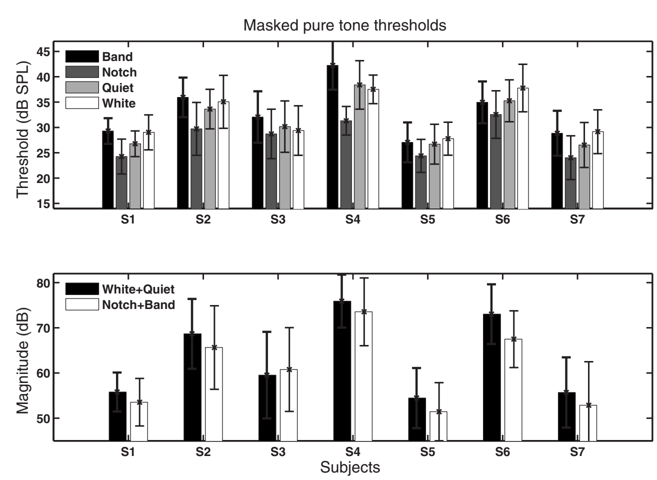

FIG. 6. Masked pure tone thresholds in each precursor condition for seven subjects. The top panel shows individual subjects thresholds in each condition averaged across frequencies. The bottom panel shows the combined thresholds I_N+I_B and I_W+I_Q for each subject (error bars represent standard deviation across frequency).

words, whether the relation $I_N+I_B=I_W+I_Q$ holds (I_Q is included to factor in the effect to the simultaneous notched-noise masker). The improvement due to the notch is significantly larger than this combined effect by 2.5 dB (two-way ANOVA with combined thresholds and frequency as factors, $p=0.015$, $N=7$, df=1, and $F=11.4$). Note that this comparison implies that additivity does not hold under these conditions and that the combined effects of these various precursors point to an underlying non-linear mechanism.

IV. DISCUSSION

The premise of this work was that the perception of a tone is affected by central gain-adaptation mechanisms and that this adaptation would be affected by the amount of cochlear compression: A more compressive cochlea would reduce the intensity difference between a loud and a quiet stimulus, and thus, changes in neuronal gain following changes in signal intensity should be less pronounced. Indeed, neuronal gain adaptation has been demonstrated in the inferior colliculus (Dean *et al.*, 2005) and auditory nerve (Wen *et al.*, 2009).

Here, gain adaptation was assessed by the sensitization observed following a notched-noise precursor, and cochlear compression was assessed using DPOAEs emitted at various primary input levels. Contrary to our expectation, no significant correlation was found between the measure of DPOAE compression and sensitization as measured by the difference between primed narrow-band and primed notched-noise thresholds. However, this sensitization did correlate with the DPOAEs measured with the lowest level primary (see Fig. 5, bottom panel). This suggests that this sensitization is affected or depends on the amplification mechanism of outer hair cells.

The sensitization phenomenon, which can be considered a form of release from masking, is unique in that sensitivity is increased when adding a sound to a probe signal—rather than decreased as is typically the case in masking.

The interpretation of this effect as the result of a neurally mediated adaptive gain is supported by the non-linearity of the combined effects of the notched- and bandpass-noise precursor conditions, as well as the long time scale over which this effect occurs. Note that sensitization is observed here as late as 250 ms after the precursor signal. This is much longer than the instantaneous effect of cochlear compression, longer than the rate adaptation for single auditory nerve fibers, and still longer than forward masking (Meddis and O'Mard, 2005). Thus, we speculate that sensitization is determined more centrally but mediated to some extent by adjusting OHC amplification gains via an efferent feedback loop.

An alternative hypothesis is that the decrease in threshold using a notched-noise precursor may result from a perceptual grouping of the precursor and masker. In this scenario the notched-noise precursor and masker are grouped together in the auditory system, resulting in the increased detectability of the target stimulus (Bregman, 1990). To test this hypothesis, a notched-noise precursor with a different spectrum from that of the masker could be used in order to control such effects and will be investigated in a future experiment.

Overall, the results show that sensitization occurs after presentation of a notched-noise masker and the strength of this sensitization correlated with DPOAEs elicited by the lowest primary level. Additionally, evidence of cochlear compression based on DPOAE I/O functions correlated strongly with both notched- and bandpass-noise psychoacoustic thresholds. In eight of ten subjects these measures correlated significantly across frequency (significance could be established despite a relatively small sample of frequencies).

V. CONCLUSIONS

In normal hearing subjects, notched noise increases sensitivity to tones embedded in noise. This increased sensitization was found to be a non-linear effect, consistent with our hypothesis of a neurally mediated gain-adaptation mechanism. However, perceptual grouping cannot be ruled as a potential mechanism. The correlation between this sensitization and DPOAEs measured with the lowest primary level is interpreted as a link between outer hair cell function and gain adaptation. Cochlear compression correlated strongly with various perceptual thresholds. This establishes DPOAE compression as a potential candidate for the objective evaluation of hearing.

ACKNOWLEDGMENTS

The authors would like to thank Zhenya Yubiler and Naomi Eichorn for their contribution to data collection efforts. This work is supported by the Tinnitus Research Initiative (TRI) and the Graduate Center of the City University of New York.

Bregman, A. (**1990**). *Auditory Scene Analysis: The Perceptual Organization of Sound* (MIT, Cambridge, MA).

Carlyon, R. (**1989**). "Changes in the masked thresholds of brief tones produced by prior bursts of noise," Hear. Res. **41**, 223–235.

Cooper, N., Pickles, J., and Manley, G. (**2008**). "Traveling waves, second filters, and physiological vulnerability: A short history of the discovery of active processes in hearing," *Springer Handbook of Auditory Research* (Springer, New York).

Dean, I., Harper, N. S., and McAlpine, D. (**2005**). "Neural population coding of sound level adapts to stimulus statistics," Nat. Neurosci. **8**, 1684–1689.

Dean, I., Robinson, B., Harper, N. S., and McAlpine, D. (**2008**). "Rapid neural adaptation to sound level statistics," J. Neurosci. **28**, 6430–6438.

Janssen, T., Kummer, P., and Arnold, W. (**1998**). "Growth behavior of the 2 f1-f2 distortion product otoacoustic emission in tinnitus," J. Acoust. Soc. Am. **103**, 3418–3430.

Kummer, P., Janssen, T., and Arnold, W. (**1998**). "The level and growth behavior of the 2 f1 f2 distortion product otoacoustic emission and its relationship to auditory sensitivity in normal hearing and cochlear hearing loss," J. Acoust. Soc. Am. **103**, 3431–3444.

Long, G. R., Talmadge, C. L., and Lee, J. (**2008**). "Measuring distortion product otoacoustic emissions using continuously sweeping primaries," J. Acoust. Soc. Am. **124**, 1613–1626.

Mauermann, M., and Kollmeier, B. (**2004**). "Distortion product otoacoustic emission (DPOAE) input/output functions and the influence of the second DPOAE source," J. Acoust. Soc. Am. **116**, 2199–2212.

Meddis, R., and O'Mard, L. (**2005**). "A computer model of the auditory-nerve response to forward-masking stimuli," J. Acoust. Soc. Am. **117**, 3787.

Neely, S., and Kim, D. (**2008**). "Cochlear models incorporating active processes," *Springer Handbook of Auditory Research* (Springer, New York).

Parra, L., and Pearlmutter, B. (**2007**). "Illusory percepts from auditory adaptation," J. Acoust. Soc. Am. **121**(3), 1632–1641.

Rosengard, P., Oxenham, A., and Braida, L. (**2005**). "Comparing different estimates of cochlear compression in listeners with normal and impaired hearing," J. Acoust. Soc. Am. **117**(5), 3028–3041.

Shera, C. A. (**2004**). "Mechanisms of mammalian otoacoustic emission and their implications for the clinical utility of otoacoustic emissions," Ear Hear. **25**, 86–97.

Strickland, E. A. (**2004**). "The temporal effect with notched-noise maskers: Analysis in terms of input-output functions," J. Acoust. Soc. Am. **115**, 2234–2245.

Taylor, M. M., and Creelman, C. D. (**1967**). "Pest: Efficient estimates on probability functions," J. Acoust. Soc. Am. **41**, 782–787.

Thibodeau, L. M. (**1991**). "Performance of hearing-impaired persons on auditory enhancement tasks," J. Acoust. Soc. Am. **89**, 2843–2850.

Viemeister, N., and Bacon, S. P. (**1982**). "Forward masking by enhanced components in harmonic complexes," J. Acoust. Soc. Am. **71**(6), 1502–1507.

Wen, B., Wang, G. I., Dean, I., and Delgutte, B. (**2009**). "Dynamic range adaptation to sound level statistics in the auditory nerve," J. Neurosci. **29**, 13797–13808.

Williams, E. J., and Bacon, S. P. (**2005**). "Compression estimates using behavioral and otoacoustic emission measures," Hear. Res. **201**, 44–54.

Zwicker, E. (**1965**). "Temporal effects in simultaneous masking by white-noise bursts," J. Acoust. Soc. Am. **37**, 653–663.