Auditory filter tuning inferred with short sinusoidal and notched-noise maskers

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The physiology of the medial olivocochlear reflex suggests that a sufficiently long stimulus (>100 ms) may reduce cochlear gain and result in broadened frequency selectivity. The current study attempted to avoid gain reduction by using short maskers (20 ms) to measure psychophysical tuning curves (PTCs) and notched-noise tuning characteristics, with a 4-kHz signal. The influence of off-frequency listening on PTCs was evaluated using two types of background noise. Iso-level curves were derived using an estimate of the cochlear input/output (I/O) function, which was obtained using an off-frequency masker as a linear reference. The influence of masker duration on PTCs was assessed using a model that assumed long maskers (>20 ms) evoked gain reduction. The results suggested that the off-frequency masker was a valid linear reference when deriving I/O functions and that off-frequency listening may have occurred in auditory filters apical to the signal place. The iso-level curves from this growth-of-masking study were consistent with those from a temporal-masking-curve study by Eustaquio-Martin and Lopez-Poveda [*J. Assoc. Res. Otolaryngol.* **12**, 281–299. (2011)], suggesting that either approach may be used to derive iso-level curves. Finally, model simulations suggested that masker duration may not influence estimates of frequency selectivity. © 2012 Acoustical Society of America. [<http://dx.doi.org/10.1121/1.4746029>]

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I. INTRODUCTION

A fundamental process in the peripheral auditory system is the decomposition of sound into individual frequency components. The frequency-resolving power of the cochlea plays a major role in the neural representation of sound, given that tonotopic coding is maintained throughout the central auditory nervous system (for a review, see [Pickles, 2008](#)). Peripheral frequency selectivity has been measured physiologically by observing how an auditory neuron, or a given location on the basilar membrane, responds to isolated tones of differing frequencies (e.g., [Rhode, 1971](#); [Liberman, 1978](#)). Behavioral techniques typically require two stimuli to measure frequency selectivity (e.g., [Wegel and Lane, 1924](#); [Fletcher, 1940](#); [Egan and Hake, 1950](#); [Small, 1959](#); [Glasberg and Moore, 1990](#); [Yasin and Plack, 2003](#); [Oxenham and Shera, 2003](#)); namely a signal and a masker. The sinusoidal signal is presented to ensure cochlear excitation cues fall within one auditory filter ([Fletcher, 1940](#)). Masking thresholds are then measured for several spectral manipulations of the masker and these thresholds are used to estimate the bandwidth of the auditory filter ([Patterson, 1976](#)). It is often assumed that behavioral techniques are sensitive to measuring the frequency selectivity of the cochlea (for a review, see [Oxenham and Wojtczak, 2010](#)). This has been supported by data showing that behavioral measures of frequency selectivity broaden with temporary or permanent cochlear hearing impairment ([Florentine et al., 1980](#); [Feth et al., 1980](#); [Glasberg and Moore, 1986](#); [Beveridge and Carlyon, 1996](#)). Forward masking approaches are often adopted to

avoid the effect of suppression of the signal by the masker, which is unavoidable in simultaneous masking. Such an approach has been argued to facilitate an appropriate comparison between psychophysical and physiological estimates of frequency selectivity ([Oxenham and Shera, 2003](#)).

Some early studies on frequency selectivity in forward masking were concerned with the effect of masker duration. For example, [Bacon and Jesteadt \(1987\)](#) measured frequency selectivity using masker durations of 50 and 400 ms. They hypothesized that any differences in frequency selectivity with masker duration were due to processing in the auditory periphery. Such processing included neural adaptation and dynamic changes in cochlear tuning. They found that frequency selectivity increased with a longer masker, suggesting that auditory filters sharpened with time.

More recently, another hypothesis has emerged to explain why frequency selectivity appears to change when the auditory system is stimulated ([Strickland, 2001, 2004](#)). Physiological studies suggest that the gain of the active process in the cochlea adapts to sound (e.g., [Siegel and Kim, 1982](#)). This adaptation results from a reflex mediated by olivocochlear fibers traveling from the brainstem to the cochlear outer hair cells and is known as the medial olivocochlear (MOC) reflex. When stimulated, the MOC reflex decreases the gain of the cochlear input/output (I/O) function, elevates the tip of the tuning curve, and leads to a reduction in frequency selectivity (e.g., [Cooper and Guinan, 2006](#)). Behavioral studies have attempted to elicit the MOC reflex and evaluate its effects on frequency selectivity by presenting an additional stimulus before the masker (i.e., a “precursor”). Such studies suggest that a precursor may decrease frequency selectivity ([Strickland, 2001](#); [Jennings et al., 2009](#)).

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The aim of the present paper is to measure frequency selectivity at several intensities in a condition where the MOC reflex is unlikely to influence the data. The stimuli in this study are based on the time course of that reflex. Otoacoustic emission (OAE) measurements (Backus and Guinan, 2006) suggest the MOC reflex exhibits an onset delay of approximately 20–25 ms. In other words, the influence of the reflex is not present until 20–25 ms after the onset of the elicitor. Given these data, previous experiments from our laboratory have used 20-ms maskers (e.g., Jennings *et al.*, 2009; Roverud and Strickland, 2010; Jennings and Strickland, 2010). Thus, when the signal is presented immediately following this short masker ($\Delta t = 0$), detection likely occurs before the MOC reflex has been elicited. A 20-ms masker is shorter than the maskers used in previous studies evaluating the effects of masker duration (e.g., Kidd *et al.*, 1984; Bacon and Jesteadt, 1987).

Behavioral measurements of frequency selectivity are likely influenced by several factors in addition to the MOC reflex. For example, the measurement technique may be one such factor, as was suggested by Bacon and Jesteadt (1987). They measured growth of masking (GOM) functions for several masker frequencies surrounding their 1-kHz sinusoidal signal. From these data they expressed frequency selectivity in two ways. First, they held the masker level constant and plotted the signal threshold as a function of masker frequency. This plot, called an “input filter pattern,” specifies the amount of masking produced by a masker of a constant level. Next, while holding the signal level constant, they plotted masker threshold as a function of masker frequency. In other words, they plotted a psychophysical tuning curve (PTC). If the cochlea were a linear system, these two expressions of frequency selectivity (i.e., input filter patterns and PTCs) should be inversely related. However, the cochlear response is compressive at mid-to-high intensities; thus, this relationship does not hold, as has been recently shown by Eustaquio-Martin and Lopez-Poveda (2011). This suggests that cochlear compression should be considered when interpreting behavioral estimates of frequency selectivity, especially at mid-to-high intensities.

The influence of compression on behavioral measurements of frequency selectivity is important when comparing psychophysical and physiological-based measures. For example, Eustaquio-Martin and Lopez-Poveda (2011) argued that it is inappropriate to compare behavioral PTCs with iso-level curves measured from the basilar membrane. To facilitate comparison between these two measures, they argued that PTCs must first be transformed to iso-level curves to account for the influence of compression. They demonstrated that such a transformation produced estimates of frequency selectivity that varied with stimulus level [30–65 dB sound pressure level (SPL) in their study] in a way similar to physiological studies (e.g., Ruggero, 1992). Specifically, these level effects consisted of broader bandwidths and shifted filter tips, although the magnitude of these effects were not as large as commonly observed in physiological studies (Ruggero, 1992; Ruggero *et al.*, 1997).

Behavioral measures of frequency selectivity may also be influenced by off-frequency listening. The power spec-

trum model of masking (Fletcher, 1940) assumes that the signal is detected through an auditory filter centered on the cochlear location that responds best to the signal. This location is hereafter referred to as the “signal place.” When the signal is detected through auditory filters remote to this location, off-frequency listening has occurred. Several techniques have been developed to limit off-frequency listening. For example, an additional background noise is often added when measuring PTCs (Patterson and Nimmo-Smith, 1980; O’Loughlin and Moore, 1981; Green *et al.*, 1981; Nelson *et al.*, 1990, 2001). It is assumed that this background noise masks the auditory filters remote to the signal place, ensuring that these filters are not used to detect the signal. Similarly, the notched-noise method (Patterson, 1976) was developed to avoid off-frequency listening by simultaneously presenting masker energy at frequencies both above and below the signal frequency. Finally, off-frequency listening is minimized in the temporal masking curve (TMC) technique (e.g., Nelson *et al.*, 2001; Yasin and Plack, 2003; Eustaquio-Martin and Lopez-Poveda, 2011) due to the use of a low-level signal, resulting in a relatively small spread of excitation. In this technique, a temporal gap is inserted between the signal and the masker. For a given gap duration, the signal is held constant at a low level, and masker threshold is measured as a function of masker frequency. As the temporal gap increases, the masker level at threshold increases. Thus, by manipulating gap duration, the TMC technique is able to assess the effects of stimulus intensity on frequency selectivity. Although this technique does control for off-frequency listening, it is possible that the MOC reflex may influence estimates of frequency selectivity obtained using the TMC technique due to the delay between the masker and signal (Wojtczak and Oxenham, 2009, 2010).

Only a handful of studies have measured PTCs with short maskers (e.g., Kidd *et al.*, 1984; Bacon and Jesteadt, 1987; Jennings *et al.*, 2009). These studies have been limited to a small set of signal levels and conditions. Moreover, there has yet to be a study measuring notched-noise tuning characteristics (NNTCs) with short maskers. The current study measured PTCs and NNTCs with a 20-ms masker across a range of signal levels. This approach satisfied the following aims: (1) assess whether short maskers avoid the influence of gain reduction, (2) assess the influence of off-frequency listening on PTCs obtained with two types of background noise, each designed to limit off-frequency listening, (3) demonstrate a technique for deriving iso-level curves from GOM data, and (4) evaluate the potential effects of masker duration on PTCs using a simple cochlear compression model that includes gain reduction. This model is based on the assumption that the MOC reflex reduces cochlear gain when the masker is sufficiently long (e.g., >100 ms). In a related paper (Jennings and Strickland, 2012), the effects of an on-frequency precursor on frequency selectivity are evaluated. Some of the data in the present experiment are also presented in that paper; therefore there is some overlap in the data among the two papers. Specifically, the overlapping data are the PTCs in the basal/apical condition (described below, open symbols in Fig. 3) and the NNTC data (Fig. 1).

FIG. 1. (Color online) NNTCs (symmetric notch conditions) as a function of signal level in five subjects. Signal level in dB SPL is displayed in the legend. The panels represent individual subjects. All normalized notch widths (x -axis) were symmetric around the center frequency (4 kHz). For visual clarity, asymmetric notch widths for S1, S3, and S4 are not plotted; however, they were included in fitting the data.

II. METHODS

A. Subjects and procedure

Six normal-hearing adults served as subjects in the experiment. Prior to enrollment in the study, subjects were evaluated using a battery of audiometric tests to rule out the presence of a hearing loss. This battery consisted of a case history, otoscopy, pure tone audiometry, tympanometry, and distortion product OAEs. Subjects having normal middle ear function and detection thresholds below 15 dB hearing level for audiometric frequencies (i.e., 500–8000 Hz) were enrolled in the study. A training period preceded data collection. This period lasted approximately 8–10 h. During the training period, subjects participated in a representative sample of the conditions described in the experiments. Subjects were paid for their participation. When subjects were recruited, they were initially assigned to either the PTC or NNTC experiment. After completing their assigned experiment, the subjects were invited to participate in the other experiment (e.g., a subject who completed the PTC experiment would then be invited to participate in the NNTC experiment). One subject (S5) elected not to participate in

the additional experiment. Two of the subjects (S4 and S6) graduated from the university and were no longer available to complete the additional experiment.

All experiments took place in a sound-attenuated room using Tucker-Davis Technologies (TDT, Alachua, FL) hardware. Stimuli were generated digitally (sampling frequency = 25 kHz), output to four separate D/A channels (TDT DA3-4, 16-bit), low-pass filtered at 10 kHz (TDT FT5 and FT6-2), mixed (TDT SM3), sent to an ER-2 insert earphone via a headphone buffer (TDT HB6), and finally to the subject's right ear. These earphones have a flat frequency response at the eardrum between 250 and 8000 Hz. Detection thresholds were measured using a three alternative forced choice procedure that estimated 70.7% correct on the psychometric function (Levitt, 1971). During a given trial, the subject heard three listening intervals marked visually on the computer screen and separated by 500 ms. Two of these listening intervals contained only the masker. In the other interval (chosen randomly) the signal and masker were presented. The subject pressed a button to indicate the interval in which the signal was perceived. Feedback was given to indicate a correct or incorrect response. Fifty trials were presented to estimate threshold. The step size was 5 dB until the second reversal, after which it decreased to 2 dB. A reversal was defined as a change in the step direction (i.e., from a high intensity toward a lower intensity or vice versa). To calculate the threshold for a given run, the stimulus level for all reversals at the smaller step size were averaged. If the total number of reversals at the smaller step size was an odd number, the first of these reversals was discarded and the remaining reversals were averaged. A threshold search was rejected under the following conditions: (1) The standard deviation was greater than 5 dB or (2) the signal was correctly identified at the upper limits of the measurement equipment (95 dB SPL in the PTC experiment, and 89 dB SPL in the NNTC experiment) over two consecutive trials. For each condition, at least four thresholds were averaged to obtain the final threshold value.

B. PTCs

As noted in Sec. I, the PTC technique involves holding the signal level constant and measuring masker threshold as a function of masker frequency. Forward masked PTCs were obtained using a 4 kHz signal. The signal was 6 ms (3 ms $\cos^2$ rise/fall ramps) in duration and occurred immediately after ($\Delta t = 0$) the 20-ms sinusoidal masker (5 ms $\cos^2$ rise/fall ramps). Signal thresholds in quiet were 21.54, 20.00, 25.20, 24.31, 22.24 and 24.50 dB SPL for subjects S1–S6, respectively. PTCs were measured for a series of signal levels ranging from 35 to 65 dB SPL in 5 or 10 dB steps. The lowest level of this range (35 dB SPL) is between 10 and 15 dB sensation level (SL) across subjects. Masker frequencies ranged from one octave below to one-quarter octave above the signal frequency. The dependent variable was masker level at threshold. Off-frequency listening (Johnson-Davies and Patterson, 1979; O'Loughlin and Moore, 1981) was limited by presenting noise simultaneously with the masker and signal. This noise will be referred to as the “off-frequency

listening noise.” PTCs were measured with two types of off-frequency listening noise where the spectrum level was 50 dB below the signal level (Nelson *et al.*, 2001). The first set of PTCs was obtained with a noise whose spectrum had a high-pass characteristic. This approach restricts off-frequency listening in cochlear regions basal to the signal place; thus these PTCs will be referred to as “basal-restricted” PTCs. Nelson *et al.* (2001) used a similar approach and showed that such a noise was effective at restricting off-frequency listening when the masker was at and below the signal frequency. The second set of PTCs was obtained with a noise whose spectrum varied according to the masker frequency. For example, for maskers below the signal frequency, the noise had a high-pass characteristic. Similarly, for maskers above the signal frequency the noise had a low-pass characteristic. Finally, for the masker at the signal frequency, the noise had a notched characteristic. This approach is similar to Oxenham and Plack (1997) and restricts off-frequency listening in cochlear regions basal and apical to the signal place. Thus, these PTCs will be referred to as “basal/apical-restricted” PTCs. The cutoff frequencies for the high-pass, low-pass, and notched noises were similar to those used by Oxenham and Plack (1997). Specifically, these cutoff frequencies were $0.9 * f_s$ for the low pass noise and $1.2 * f_s$ for the high pass noise, where f_s is the signal frequency. The off-frequency listening noise was generated in the frequency domain and was gated on 50 ms before the onset of the masker and off 50 ms after the offset of the signal. For one subject (S1), the high-pass noise was not effective in restricting off-frequency listening when the masker frequency was just below the signal frequency (i.e., when the masker was 3750 Hz). For this particular subject and condition a notched off-frequency listening noise was used instead of the high-pass noise. The signal level was randomized during data collection, and basal-restricted PTCs were collected first in all subjects.

C. NNTCs

The notched-noise method provides an alternative technique for measuring frequency selectivity and is thought to be less susceptible to off-frequency listening (Patterson, 1976). The temporal characteristics of the signal and masker were the same as the PTC experiment, except the masker was a notched noise instead of a sinusoid. The spectral parameters of the notched noise were set according to Oxenham and Simonson (2006). Specifically, the notched noise was created by generating two bands of noise, one above the signal frequency (high-frequency noise band) and the other below the signal frequency (low-frequency noise band). These bands of noise were generated independently in the frequency domain, and frequency components outside of the passbands were set to zero. High and low-frequency noise bands had a bandwidth of 1000 Hz. Frequency selectivity was measured by introducing a series of spectral notches between the high- and low-frequency noise bands. The notch width (Δf) was normalized relative to the signal frequency where $\Delta f = |f_c - f_s|/f_s$. Specifically Δf specifies the spectral distance between the signal frequency and the cutoff frequencies (f_c) for the high- and low-frequency noise bands.

The following normalized notch widths were tested: 0.0, 0.025, 0.05, 0.1, 0.2, 0.3, and 0.4. Asymmetric-notch conditions were also tested in three subjects (S1, S3, and S4) where upper and lower normalized deviations were 0.1 and 0.3, 0.2 and 0.4, 0.3 and 0.1, or 0.4 and 0.2. Thresholds for these conditions were also used in estimating auditory filter shapes (Sec. III A); however, many thresholds for high-level signals reached the maximum output of the equipment. Given this observation and the lack of asymmetric-notch conditions for S2 and S5, the discussion of the data will focus on the symmetric-notch conditions. As with previous forward masking studies (Oxenham and Shera, 2003; Oxenham and Simonson, 2006), it was assumed that the notched-noise method restricted off-frequency listening. Thresholds for each signal level were obtained in random order.

III. DATA ANALYSIS

A. Estimating filter bandwidths

Filter sharpness was estimated from PTCs and NNTCs by assuming roex (pwtp) filter shapes (Patterson *et al.*, 1982). For the PTCs, each side (i.e., lower tail or upper tail) of the tuning curve was fit separately as follows:

$$W(f_l) = \theta_{BF} - 10 * \log_{10}[(1 - w_l)(1 + p_l|g|)e^{-p_l|g|} + w_l(1 + t_l|g|)e^{-t_l|g|}], \quad (1)$$

$$W(f_u) = \theta_{BF} - 10 * \log_{10}[(1 + p_u|g|)e^{-p_u|g|}], \quad (2)$$

where $g = f - BF/BF$, p (“ p_l ” or “ p_u ”) and t (“ t_l ” or “ t_u ”) determined the filter slopes at the tip and tail respectively, w (“ w_l ” or “ w_u ”) determined the intersection of these two slopes and θ_{BF} was the masker threshold at the tip [i.e., the best frequency (BF)] of the PTC.

NNTCs were fit with roex filter shapes under the assumptions of the power spectrum model of masking (Fletcher, 1940) similar to many previous studies (e.g., Glasberg *et al.*, 1984; Rosen *et al.*, 1998; Oxenham and Shera, 2003) as follows:

$$W(f_l) = (1 - w)(1 + p_l|g|)e^{-p_l|g|} + w(1 + t_l|g|)e^{-t_l|g|}, \quad (3)$$

$$W(f_u) = (1 + p_u|g|)e^{-p_u|g|}, \quad (4)$$

where the interpretation of p_u , p_l , t_l , and w is equivalent to the PTC fitting procedure. Roex filter parameters were estimated using a least squares method. The best fitting parameters and the resulting root-mean-square (rms) error calculations are presented in the Appendix. One advantage of the PTC method over the notched-noise method is the ability to observe changes in the tip frequency of the auditory filter. This becomes important when evaluating the relationship between frequency selectivity and stimulus level. For example, physiological studies have reported a consistent shift in tip frequency with increasing stimulus level (e.g., Ruggero *et al.*, 1997). Such a shift cannot be observed using the notched-noise technique.

Filter sharpness was derived from the roex fits and was expressed as the “quality factor” (Q). Specifically, Q equals the filter’s center frequency divided by its bandwidth at a predetermined dB value above θ_{BF} . Common Q values include bandwidths at 3 and 10 dB above θ_{BF} (denoted Q_3 and Q_{10}). The trends for Q_3 and Q_{10} were similar in the current paper; therefore, only Q_3 values are presented.

B. Estimating cochlear I/O functions

A subset of the PTC data was used to estimate the cochlear I/O function using the GOM technique (Oxenham and Plack, 1997). This subset included PTC thresholds for the 2500 Hz masker, as well as additional data where GOM was measured down to 5 dB SL for this masker frequency. In the present study, GOM was measured for masker frequencies at and well below the signal frequency. When the masker frequency is well below the signal frequency (~ 1 octave), the resulting GOM function is non-linear in normal hearing listeners. This non-linear GOM function is often interpreted as an estimate of the I/O function at the signal place (Oxenham and Plack, 1997). Data measured with the GOM technique are thought to resemble direct measurements of the basilar membrane in experimental animals (Oxenham and Plack, 1997). Interpreting GOM data as an estimate of the cochlear I/O function hinges on an assumption that the excitation of the “off-frequency” masker grows linearly at the signal place creating a linear reference. Recent TMC studies suggest that this assumption may be valid only for high-frequency signals and for maskers at least an octave below the signal frequency (Lopez-Poveda *et al.*, 2003; Lopez-Poveda and Alves-Pinto, 2008). These studies suggest that the growth of the masker becomes shallow at high levels when the masker frequency is not low enough. As a result the cochlear I/O function estimated using a nonlinear reference exhibits less compression than the true cochlear I/O function. Although the assumption of a linear reference has not been evaluated using the GOM technique, the findings from the above TMC studies have been assumed to apply to data measured with GOM.

In the current study, GOM functions were not well defined for a masker an octave below the signal frequency. This is due to the use of short maskers, which generally produce less masking than long maskers. Thus, for a given signal level, masker thresholds may be higher for a short masker than a long masker. Since short maskers produce higher thresholds, as the signal level increases, a short masker will reach the limits of the measurement equipment at a lower signal level than would a long masker. This effectively reduces the range of signal levels where GOM can be measured with a short masker, especially for masker frequencies far from the signal frequency. Given these circumstances, data from the 2.5 kHz masker were used to derive the I/O functions (except for S6 where this value was 3.0 kHz). This frequency was chosen because GOM could be measured up to a reasonably high signal level (~ 60 dB SPL) without reaching the maximum output of the masker (95 dB SPL).

A popular model used to fit off-frequency GOM functions consists of a piecewise linear function (or so-called “broken stick function”) that intersects at a breakpoint (Yasin and Plack, 2003). Although this model often fits well, it does not account

for the sharp roll off in GOM functions observed near absolute threshold. In theory, this sharp roll off may be due to masking produced by internal (i.e., physiological) noise within the subject. In other words, as the signal level approaches absolute threshold, the internal noise may serve as an additional masker and result in lower than expected masker levels (Humes and Jesteadt, 1989). Jennings and Strickland (2010) modified the broken stick function to account for the sharp roll off in GOM functions by including an additional parameter intended to account for this internal noise. Off-frequency GOM functions were fit using this modified approach and expressed in intensity units as defined by

$$I_y = I_g(I_x - I_\theta) \quad I_x \leq b, \quad (5)$$

$$I_y = (I_x - I_\theta)^c * I_k * I_g \quad I_x > b, \quad (6)$$

where I_y is the predicted masker intensity, I_x is the input signal intensity, I_g , c , I_b , and I_θ are model parameters representing gain, compression exponent, breakpoint, and internal noise, respectively, and $I_k = 10^{b*(1-c)}$. All terms except the compression and breakpoint (b) parameters are expressed in intensity units. In the current study the estimates of the cochlear I/O function were used to derive iso-level curves similar to those presented in Eustaquio-Martin and Lopez-Poveda (2011). It was assumed that the 2500 Hz masker produced a linear response at the signal place. An analysis of the validity of this assumption is presented in Sec. IV. This analysis is based on the hypothesis that any off-frequency non-linearity occurs central to the basilar membrane (e.g., Plack and Arifanto, 2010), as cochlear physiology does not exhibit off-frequency non-linearity. For example, Ruggero *et al.* (1997) measured the response of the basal portion of the cochlea in non-human animals and found that sinusoids 0.7 octaves below the CF produced a linear response up to the highest level tested (90 dB). Given this observation, several studies (Lopez-Poveda *et al.*, 2005; Lopez-Poveda and Eustaquio-Martin, 2006; Plack and Arifanto, 2010) hypothesized that the inner hair cell (IHC) receptor potential may be responsible for the shallow growth of the off-frequency masker at high levels. If this hypothesis were true, the effects of the IHC receptor potential would equally influence the response growth to other masker frequencies. Therefore, a potential approach to remove the confounding influence of the IHC receptor potential is to plot the masker thresholds for the off-frequency masker as a function of the masker thresholds for the on-frequency masker (i.e., the masker with the same frequency as the signal). This approach was used in the current study to check the validity of the fitted off-frequency GOM functions. Specifically, the GOM functions were fit using Eqs. (5) and (6) while assuming the off-frequency masker was an appropriate linear reference. Then the masker thresholds for the off-frequency masker were plotted as a function of the masker thresholds for the on-frequency masker. In such a plot, the influence of the IHC receptor potential should cancel because it applies to both masker frequencies. Finally, the fitted GOM function was plotted on the same plot and then shifted vertically to match the data. This shifting is done to account for the listener’s

FIG. 2. (Color online) Estimates of filter sharpness (Q_3) derived from NNTCs assuming roex (pwtp) filter shapes.

criterion signal-to-masker ratio. Since the independent variables are different between plots (one being signal level and the other the on-frequency masker level) the dependent variables should differ by this ratio. If the shifted GOM function overlaps with the data, this suggests that the off-frequency masker was an appropriate linear reference.

C. Assessing off-frequency listening

The PTC data were analyzed to check the efficacy of limiting off-frequency listening by presenting background noise. This analysis compared PTCs obtained with the two types of off-frequency listening noise discussed earlier. The upward spread of excitation is thought to be a major factor in off-frequency listening (Nelson *et al.*, 2001). As the signal level increases, the excitation elicited by the signal spreads toward the base of the cochlea (Von Békésy, 1960). If upward spread of excitation were the only factor in facilitating off-frequency listening, there should be little difference between basal and basal/apical-restricted PTCs. Alternatively, if the signal produces spectral splatter, or if there is some “downward” spread of excitation, listeners may use this additional excitation to detect the signal through auditory filters apical to the signal place. Thus, the extent in which basal and basal/apical-restricted PTCs differ may reveal the extent to which off-frequency listening occurred in these apical filters.

FIG. 3. (Color online) Basal (closed symbols) and basal/apical-restricted (open symbols) PTCs as a function of signal level in four subjects. Each column of panels represents a different subject. Signal level in dB SPL is displayed in each panel.

IV. RESULTS

A. NNTCs

NNTCs as a function of signal level are presented in Fig. 1, where each panel displays data from a different subject. At high levels, some NNTCs are incomplete (e.g., S1 and S2) due to the highest masker level reaching the maximum output of the system (89 dB SPL, or 56 dB spectrum level). When comparing NNTCs for a given signal level across subjects (e.g., comparing triangles) the effects of inter-subject variability are apparent. Given this variability, the data were analyzed for each subject individually rather than averaging the data across subjects. Estimates of filter sharpness (Q_3) obtained from the roex fits are plotted in Fig. 2. Statistical tests regarding the effects of signal level on NNTC bandwidth were not performed because Q_3 values were common among three or more subjects for only two signal levels (i.e., 45 and 50 dB SPL). In general, Q_3 appears to increase slightly with the level of the notched-noise masker (except for S3 at 60 dB SPL). These results are consistent with Eustaquio-Martin and Lopez-Poveda (2011) who also measured frequency selectivity at 4 kHz using NNTCs. However, the results contrast with Oxenham and Simonson (2006) who reported a slight increase followed by a decrease in frequency selectivity with stimulus level. Although Oxenham and Simonson (2006) reported a significant main effect for stimulus intensity across four signal frequencies, *post hoc* testing revealed that this effect was insignificant at 4 kHz. Thus, from this and previous studies it is difficult to draw a solid conclusion regarding the effect of stimulus level on NNTCs measured at 4 kHz. As suggested by Eustaquio-Martin and Lopez-Poveda (2011), the effects of cochlear compression may contribute to this difficulty. In other words, if the NNTCs were transformed to correct for compression, the effect of stimulus level on frequency selectivity may be more obvious. Transformed NNTCs were obtained in the current experiment and are discussed in Sec. IV D.

FIG. 4. (Color online) Estimates of filter sharpness (Q_3) for basal (B) and basal/apical (A) restricted PTCs. Symbols represent individual subjects.

B. PTCs

Basal-restricted (closed symbols) and basal/apical-restricted (open symbols) PTCs are presented in Fig. 3 where each column of panels represents a different subject. The SPL of the signal or “probe” (L_p) is displayed in the lower left corner of each panel. Hypothetically, the difference in threshold between basal and basal/apical-restricted PTCs is due to off-frequency listening occurring in the apex of the cochlea. This difference occurs at masker frequencies greater than or equal to the signal frequency (4 kHz) and is largest for high signal levels (e.g., S1 at 50 and 55, S2 at 50 and 55, and S3 at 55 and 60 dB SPL). Moreover, this difference is largely absent at low signal levels. The stimulus conditions for maskers below the signal frequency were identical between basal and basal/apical-restricted PTCs, so the same thresholds were used in both sets of PTCs.

Estimates of filter sharpness are presented in Fig. 4 for basal and basal/apical-restricted PTCs, respectively. Lines were fit to these data to estimate the slope relating Q_3 to signal level. Basal-restricted PTCs [Fig. 4(B)] broaden with level, as the average slope of the fitted lines was statistically different than zero ($t[3] = -3.29, p = 0.046$). Conversely, frequency selectivity for basal/apical-restricted PTCs [Fig. 4(A)] showed no significant effect of signal level ($t(3) = 0.03, p > 0.05$). Finally, the average difference in Q_3 was not statistically different ($t[3] = -1.50, p > 0.05$) between basal and basal/apical-restricted PTCs, where averaging was done across signal level. Given the number of subjects in the study, the absence of a significant effect should not be interpreted as evidence that such an effect does not exist. Eustaquio-Martin and Lopez-Poveda (2011) measured PTCs at 4 kHz using the TMC technique. Their Q_3 values increased abruptly, decreased abruptly, and then continued to slowly decrease as a function of masker level. Based on their conceptual model, this abrupt increase and decrease may be a result of cochlear compression. The current study showed no such effect, despite covering a similar range of masker levels as their study. The possible origin of this discrepancy is unclear; however, it may relate to the differences between techniques (i.e., GOM vs TMC). For example, previous TMC studies have reported similar abrupt changes in frequency selectivity with stimulus level (Lopez-Poveda *et al.*, 2007); however, such an effect has rarely been observed in previous GOM studies on the same topic (i.e., Widin and Viemeister, 1979; Green *et al.*, 1981; Nelson *et al.*, 1990; Nelson, 1991) (however, see Moore, 1978). The tip frequency of some basal-restricted PTCs is shifted to a frequency lower than the signal frequency (e.g., S1 [50, 55 dB SPL], S2 [45–55 dB SPL], S3 [60 dB SPL], S6 [45–60 dB SPL]). This shift has been observed previously and has been interpreted as evidence for off-frequency listening (Moore and Alcantara, 2001; Kluk and Moore, 2004).

C. I/O function estimates and off-frequency listening

The estimated cochlear I/O functions derived by fitting the off-frequency GOM data for the 2.5-kHz masker are shown as solid lines in Fig. 5. The x - and y -axes for these functions are signal level and masker level at threshold.

FIG. 5. (Color online) Testing the validity of the assumptions used to estimate cochlear I/O functions at the signal place. I/O functions derived from the GOM technique (black solid lines) are plotted along with data from the on-frequency masker (filled triangles). (A) I/O functions estimated from the basal/apical-restricted PTCs. The overlap between the I/O function and the on-frequency masker data supports the assumption that the off-frequency masker was an appropriate linear reference. (B) I/O functions estimated from the basal-restricted PTCs. The I/O functions and the on-frequency masker data diverge suggesting that off-frequency listening was not adequately controlled (see the text).

Compression and breakpoint estimates of these functions for S1, S2, S3, and S6 were [0.62, 32.69], [0.55, 41.35], [0.39, 41.06], and [0.32, 36.67], respectively. The symbols in Fig. 5 represent the off-frequency masker thresholds plotted as a function of the on-frequency masker thresholds. The arbitrary axis labels (i.e., “Input” and “Output”) were assigned due to the lines and symbols having different x -axes. Plotting the off-frequency masker thresholds as a function of the on-frequency masker thresholds is thought to correct for any compressive effects common to both maskers, such as IHC compression (Plack and Arifanto, 2010). In Fig. 5(A) (basal/apical-restricted PTCs), the symbols lie on top of the lines, suggesting that correcting for possible IHC compression was not necessary. This finding supports the assumption that the response growth of the 2.5 kHz masker was an appropriate linear reference. Figure 5(B) displays I/O functions derived for the basal-restricted PTCs. In this case, the symbols and lines diverge; however, the divergence is likely due to off-frequency listening rather than a compressive off-frequency reference. These results suggest that basal-restricted PTCs may have been influenced by off-frequency listening. These effects may have occurred in apical auditory filters due to spectral splatter or downward spread of excitation.

D. Deriving iso-level curves

In physiology, the frequency selectivity of the basilar membrane may be estimated by measuring velocity (or displacement) as a function of frequency for a sinusoid whose level is held constant (e.g., Ruggero *et al.*, 1997). A plot of this measurement (velocity vs frequency) is called an iso-level curve. Previous psychophysical studies have attempted to measure iso-level curves using behavioral techniques (Bacon and Jesteadt, 1987; Moore and Glasberg, 2003). More recently, Eustaquio-Martin and Lopez-Poveda (2011) observed that iso-level curves could be obtained from PTCs or NNTCs after transforming the data by an estimate of cochlear compression. Iso-level curves were derived from NNTCs and basal/apical-restricted PTCs following the technique described by Eustaquio-Martin and Lopez-Poveda (2011). By definition, an iso-level curve requires that the cochlear output be defined for a fixed masker level across a range of masker frequencies or notch widths. To meet this requirement, the following assumptions were made: (1) The estimate of the cochlear I/O function described in Sec. IV C was an accurate estimate of the true cochlear I/O function, (2) for a given signal level, the masker output (through a cochlear filter centered on the signal place) at threshold is constant across masker frequency (PTC) or notch width (NNTC), and (3) the auditory filter shape was symmetric in NNTC-derived iso-level curves. Under these assumptions, the masker output for a given signal level can be obtained from the estimated cochlear I/O function. Given that the masker output at threshold is equal across masker frequencies (assumption 2), this output maps to several inputs. Specifically, these inputs are the masked thresholds measured across frequency/notch width. Thus, for a given masker frequency/notch width, a plot of the masker outputs versus the corresponding masked thresholds will reveal the I/O function for that masker at the signal place. This is shown in Fig. 6(A), where each row represents a different subject. In this plot, the abscissa is the masker level for a given frequency and the ordinate is the off-frequency masker level. Measuring frequency selectivity using the PTC method corresponds to a horizontal slice across the y -axis in Fig. 6(A). In other words, the PTC method is an “iso-response” measure since the output is held constant across frequency. In contrast, an iso-level curve is obtained by slicing vertically across the x -axis (input is held constant across frequency). Iso-level curves ranging from 40–90 dB SPL are presented in Fig. 6(B). These curves represent the response of the cochlea at the signal place to a masker whose level is held constant but whose frequency is varied. Iso-level curves displayed as colored lines (solid and dotted) were obtained from the derived I/O function presented in Fig. 6(A). Additional I/O functions for intermediary frequencies not tested were interpolated from the roex filter functions fitted to the PTC data. These additional roex-based I/O functions served to fill in the low- and high-frequency sides of the iso-level curves [thin gray lines in Fig. 6(B)].

Estimates of filter sharpness (Q_3) for the iso-level curves from transformed PTCs are presented in Fig. 7(A). The tip of some iso-level filters was undefined (e.g., S1 and S6 above

FIG. 6. (Color online) Derived cochlear I/O functions (A) and iso-level curves (B) from basal/apical-restricted PTCs. I/O functions for several masker frequencies (symbols) are plotted for four subjects (rows). These I/O functions represent the response of a masker passing through an auditory filter center at the signal frequency. Off-frequency GOM was used to derive these I/O functions (see the text). Iso-level curves were obtained by slicing vertically through the I/O functions at several input levels. Additional data points for the iso-level curves were obtained by interpolating from roex (pwtpt) functions (gray lines) fit to the data.

55 dB SPL, S2 above 70 dB SPL, and S3 above 60 dB SPL); therefore, for such cases, Q_3 could not be calculated. As expected from cochlear physiology, Q_3 generally decreased or remained constant as a function of signal level in most subjects, consistent with Eustaquio-Martin and Lopez-Poveda (2011). A comparison of Q_3 estimates obtained for PTCs and iso-level curves from transformed PTCs is presented in Fig. 7(B). Most data points lie on or to the right of the diagonal, suggesting that estimates of filter sharpness are consistently lower for derived iso-level curves compared to PTCs. This result is consistent with Eustaquio-Martin and Lopez-Poveda (2011) and supports their conclusion that PTCs are not accurate estimates of basilar membrane iso-level curves. However, it should be noted that filter sharpness is similar between derived iso-level curves and PTCs at the lowest levels tested (10–15 dB SL).

Notched-noise I/O functions and iso-level filters were estimated for subjects who had a complete data set from both PTC and NNTC experiments (S1, S2, and S3). These data are presented in Figs. 8(A) and 8(B), respectively.

Figure 9(A) displays Q_3 estimates for these iso-level curves. With the exception of two data points (S1 and S3 at 60 dB SPL), these iso-level curves are flat and are within the same range measured by Eustaquio-Martin and Lopez-Poveda (2011). The high Q_3 values from these two data points are a result of the sharp increase in threshold between the 0.0 notch width condition and the adjacent notch width condition (0.025). For comparison, the 0.025 notch width was removed [Fig. 9(B)]. This notch width was not tested in Eustaquio-Martin and Lopez-Poveda (2011) or in other recent studies (Oxenham and Shera, 2003; Oxenham and Simonson, 2006); therefore, removing this point provides a more direct comparison.

E. PTC and NNTC filter bandwidths may not correlate

Three of the subjects (S1, S2, and S3) in the present study participated in both PTC and NNTC experiments. In theory, PTC and NNTC estimates of filter sharpness should be correlated within these subjects. An informal analysis

FIG. 7. (Color online) Estimates of filter sharpness interpolated from iso-level curves derived from basal/apical-restricted PTCs. (A) Comparison of estimates of frequency selectivity between PTCs and iso-level curves from transformed PTCs (B).

suggested that this may not be true; however, formal statistical tests were not performed due to the small number of subjects. Similar conclusions were reported qualitatively by Eustaquio-Martin and Lopez-Poveda (2011); however, they did observe good agreement between derived iso-level curves (their Fig. 8). A similar analysis was not possible with the current data set due to a lack of signal levels where both measures (i.e., iso-level curves from transformed PTCs and NNTCs) could be derived.

V. MODEL SIMULATIONS

The estimates of frequency selectivity obtained in the current study were not appreciably different from previous GOM studies that used longer maskers (e.g., Green *et al.*, 1981; Nelson *et al.*, 1990; Nelson, 1991). Similarly, no obvious differences in frequency selectivity were found between the current study and studies using the TMC technique, such as Eustaquio-Martin and Lopez-Poveda (2011). Despite this, the results of Bacon and Jesteadt (1987) suggest that masker duration may influence estimates of frequency selectivity. They reported a large effect of masker duration when measuring input filter patterns; however, their results should be interpreted with caution because the data were not transformed to account for compression. For example, assume the masker is presented at a constant low level, and an input filter pattern is being measured. If the long masker produces greater masking, the signal level at threshold would increase, relative to the threshold with a short masker, until the criterion signal-to-noise ratio (SNR) was met. Maskers far from the signal frequency produce little excitation at the signal place; therefore, it is likely that signal level at threshold is on the linear portion of the I/O

function for these maskers, regardless of masker duration. Conversely, maskers near the signal frequency produce appreciable excitation at the signal place and may result in masking thresholds near or above the compression breakpoint. If the additional masking produced by a long masker results in the signal being compressed, the signal level at threshold will increase dramatically and result in a seemingly sharper masking pattern. In other words, the apparently large effect of duration on frequency selectivity observed by Bacon and Jesteadt (1987) could have been due to compression. When Bacon and Jesteadt (1987) derived PTCs from their data, the results were closer to Kidd *et al.* (1984) who found little to no effect of masker duration. This suggests that although using a short masker may control for the effects of gain reduction, the resulting estimate of frequency selectivity changes very little when measured with a long masker.

A simple basilar membrane compression model was evaluated to determine why PTCs are similar between long and short maskers. In this context, the duration of the short masker is less than the onset delay of the MOC reflex (20–25 ms). Similarly the duration of the long masker is equal to or greater than the time it takes for the MOC reflex to reach full strength (~ 200 ms). I/O functions at the signal place (4 kHz) were simulated for maskers ranging from 2000–4400 Hz using the same model as Eqs. (5) and (6). The model parameters were set so the I/O function at a given masker frequency would intersect the unity line (slope = 1, intercept = 0) at 100 dB SPL. This is a simplifying assumption that implies that there would be no frequency selectivity at 100 dB SPL, which is unlikely to occur in physiology. Given this, the model simulations are restricted to the mid-level output of the I/O functions. All I/O function parameters were set relative to the I/O function of the 4-kHz masker. The parameters for this baseline (0) function in dB were: $g_0 = 56$, $b_0 = 30$, $c_0 = 0.2$, and $\theta_0 = 15$. These values are consistent with previous psychophysical (Oxenham and Plack, 1997; Nelson *et al.*, 2001; Plack *et al.*, 2006) and physiological (Yates *et al.*, 1990; Ruggero, 1992; Ruggero *et al.*, 1997) data. The gain values for the I/O functions of other masker frequencies were based on the model described by Zilany and Bruce (2006, 2007). The basilar membrane response of this model was used because it accounts for a wide range of physiological data (Kiang, 1965; Liberman, 1978; Liberman and Dodds, 1984; Carney and Yin, 1988; Miller *et al.*, 1997). The gain applied to individual maskers g_{fm} was 0, 10, 23, 37, 46, 56, 54, 47, and 33 for 2000, 2500, 3000, 3500, 3750, 4000, 4100, 4200, and 4400 Hz maskers, respectively. The breakpoints of these I/O functions were set based on these gain values by the equation $b_{fm} = b_0 + g_0 - g_{fm}$. Similarly, the compression values of these I/O functions were defined by the equation $c_{fm} = [c_0 * (100 - b_0)] / (100 - b_{fm})$. Figure 10 displays the model I/O functions for all masker frequencies.

The I/O functions displayed in Fig. 10 were used to simulate PTCs for short and long maskers at various masker output levels. The following assumptions were implemented: (1) Detection occurred when the masker and signal reached

FIG. 8. (Color online) Derived response functions (A) and iso-level curves (B) from NNTCs. Response functions for several masker notch widths (symbols) are plotted for three subjects (rows). These response functions represent the growth of masker energy passing through an auditory filter center at the signal frequency. Off-frequency GOM was used to derive these response functions (see the text). Iso-level curves were obtained by slicing vertically through the response functions at several input levels.

a criterion SNR, (2) gain reduction did not influence detection in the short masker PTCs (i.e., the gain values of the I/O functions in Fig. 10 were constant across masker output level), and (3) gain was reduced in the long masker PTCs and the magnitude of this reduction increased with increasing masker output. Six masker outputs were evaluated and are represented by the dashed horizontal lines in Fig. 10 labeled o_1 through o_6 . This range of outputs was chosen to evaluate the effects of the breakpoint and compression on simulated PTCs. For the long masker simulation, it was assumed that gain reduction for the 4 kHz I/O function was linearly related to masker output (Brown *et al.*, 2010; Jennings *et al.*, 2011). In other words, as the masker output increased by some amount, the gain of the I/O function at 4 kHz was reduced by that same amount. The reduction in gain at other masker frequencies was scaled relative to the gain reduction at 4 kHz. This scaling procedure involved multiplying the amount of gain reduction at 4 kHz by

G_{fm}/G_0 . Finally, at the lowest masker output (o_1), it was assumed that the reduction in gain at 4 kHz was minimal and was arbitrarily set to 2 dB.

Predicted PTCs for the short and long masker simulations are shown in Fig. 11 for the masker outputs presented in Fig. 10. Short and long masker PTCs are represented by the dotted and solid lines, respectively. Estimates of frequency selectivity (Q_{10}) for a given PTC are plotted near the tip (short masker) or tail (long masker) of the PTC. At low to mid masker outputs (o_1 – o_4) the simulated PTCs deviate at the tail frequencies. This deviation results in a small reduction in frequency selectivity for the long masker PTCs relative to the short masker PTCs. At higher masker outputs (o_5 – o_6) the simulated PTCs for long maskers are vertically displaced relative to PTCs for short maskers, resulting in no difference in frequency selectivity.

The simulated PTCs suggest that estimates of frequency selectivity would not be greatly affected if the long masker

FIG. 9. (Color online) Estimates of filter sharpness interpolated from iso-level curves derived from NNTCs. (A) Q_3 values measured when all notch widths are included. (B) The same as (A) but with the 0.025 notch width excluded.

elicited gain reduction. The largest effects of reducing the gain are seen at masker outputs near the breakpoint of the I/O function. Below the breakpoint, the amount of gain reduction is too small to make a large difference in frequency selectivity. Above the breakpoint, reducing the gain shifts the entire PTC down; however, the shift is roughly constant across frequency. These results are qualitatively similar to

FIG. 10. (Color online) A schematic of the simple basilar membrane compression model used to evaluate the influence of gain reduction in measuring PTCs with short and long maskers. I/O functions for several masker frequencies are shown by solid and dashed lines. PTCs were simulated for several output values (O_1 – O_6) below, near, and above the compression breakpoint. Gain reduction was simulated by adjusting the gain of the I/O functions (see the text).

FIG. 11. Simulated PTCs for short (dashed lines) and long (solid lines) maskers. Each panel represents one of the six output values displayed in Fig. 10. Numerical values in each panel represent Q_{10} values interpolated from the predicted PTCs. Q_{10} values for the short and long maskers are plotted at the tip and tail of the PTCs, respectively.

Kidd *et al.* (1984) and Bacon and Jesteadt (1987) who reported a small difference in frequency selectivity between PTCs measured with short and long maskers. Although NNTCs were not simulated, a similar result is expected where the largest effects of reducing the gain exist at wide notch widths. Since Q_3 and Q_{10} are computed from data obtained at narrow notch widths, the effects of gain reduction are not expected to influence NNTCs measured with a long masker.

VI. DISCUSSION

The current study evaluated the effects of measuring frequency selectivity using a short masker rather than the traditional practice of using long maskers. The use of short maskers was motivated by the observation that frequency selectivity is influenced by a reduction in gain via the MOC reflex (Cooper and Guinan, 2006). It was assumed that this gain reduction would have a minimal effect on PTCs and NNTCs measured with a short masker due to the reflex's sluggish onset. Below, the results of the current study are compared with previous data. In general, frequency selectivity measured with a short masker (current study) did not

differ substantially from studies using a long masker. This was true of Q_3 estimates for commonly-measured low levels (~ 10 dB SL) and for the relationship between Q_3 and stimulus level.

A. Filter bandwidths at low signal levels

The estimates of filter sharpness from the NNTC experiment are consistent with [Oxenham and Shera \(2003\)](#). They reported a Q_{ERB} estimate of about 15 for NNTC measured at 10 dB SL. At the lowest signal level tested (~ 15 – 20 dB SL) in the present NNTC experiment, the average Q_{ERB} was 13.78. Similarly, for basal and basal/apical-restricted PTCs at the lowest level, the average Q_{ERB} values were 18.73 and 19.22, which are within the 95% confidence limits reported by [Oxenham and Shera \(2003\)](#). Recently, [Eustaquio-Martin and Lopez-Poveda \(2011\)](#) measured NNTCs and reported Q_3 values ranging from 15 at low levels (30–40 dB SPL) to 125 at the highest level (50 dB SPL) (filled black symbols in their Fig. 5). The Q_3 estimates at low signal levels in Fig. 2(A) are quantitatively similar to their study at low signal levels. Moreover, the current study also observed an increase in Q_3 with increasing signal level in the majority of subjects.

[Eustaquio-Martin and Lopez-Poveda \(2011\)](#) also reported Q_3 values for PTCs (filled gray symbols in their Fig. 5). Their estimates are lower than what was observed in the current experiment (Fig. 4) for PTCs measured at the lowest signal level. The source of the discrepancy between experiments is unknown; however, the methods for measuring PTCs were quite different between studies. For example, [Eustaquio-Martin and Lopez-Poveda \(2011\)](#) used the TMC technique and a longer masker and signal (400 and 10 ms, respectively).

One puzzling result was the lack of agreement between Q_3 values for PTCs and NNTCs within a given subject. A similar result was found by [Eustaquio-Martin and Lopez-Poveda \(2011\)](#), who argued that cochlear compression and its strong effects on iso-response measures may be to blame. They confirmed this hypothesis by deriving iso-level filters from their NNTC and PTC data. The filter shapes resulting from this derivation were nearly identical regardless of the method (i.e., NNTC vs PTC), suggesting that cochlear compression influenced the discrepancy between NNTCs and PTCs. Suppression and off-frequency listening may have also contributed to the lack of correlation between PTCs and NNTCs. For example, the noise bands used in the NNTC technique could have suppressed each other. The data from the smallest notch width (0.025) suggest this may be true. For example, mutual suppression of the noise bands would decrease the effective level of the masker. This decrease could explain the sharp increase in masker threshold from the 0.0 to the 0.025 notch widths in some NNTCs (e.g., S1 at 45 and 50 dB SPL, S3 at 45 and 55 dB SPL, S5 at 50 dB SPL). This interpretation is based on the assumptions: (1) That suppression is stronger in the small notch width condition compared to the condition without a notch and (2) that suppression decreases for notch widths wider than 0.025. Both of these assumptions are consistent with the level dependence of suppression

([Ruggero, 1992](#)) and suppression tuning curves ([Arthur et al., 1971](#)). In addition to suppression, the effect of off-frequency listening may not have been constant across NNTCs and PTCs. In the NNTC experiment, off-frequency listening was not restricted because it is often assumed that off-frequency listening does not occur in NNTCs. This assumption may have originated from early NNTC studies in simultaneous masking where off-frequency listening was less likely to occur because the masker and signal were presented simultaneously. Although this may be true for NNTCs measured in simultaneous masking, in forward masking it may not be true, especially at higher signal levels. For example, the energy of the masker decays shortly after its offset. This suggests that auditory filters remote from the signal place may become available as the masker energy decays. Further research is needed to evaluate the effect of off-frequency listening on forward-masked NNTCs measured at high signal levels. Finally, the lack of agreement between PTCs and NNTCs within a given subject may be due to the limited number of subjects who completed both PTC and NNTC experiments.

B. Filter bandwidths across stimulus levels

Basilar membrane iso-level curves measured in the base of the cochlea exhibit both a broadening and a shifted BF as a function of stimulus level ([Ruggero et al., 1997](#)). These two characteristics have been observed in PTCs above 1 kHz; however, they are eliminated when background noise is presented to restrict off-frequency listening ([Green et al., 1981](#); [Nelson et al., 1990](#)). The present PTCs (Fig. 3) show the same pattern between the basal and basal/apical-restricted PTCs; namely, that basal-restricted PTCs broaden with level and have a shifted BF, while basal/apical-restricted PTCs show constant filter bandwidths and BFs across signal level.

Broadened tuning with stimulus level has also been observed in NNTCs at 4 kHz ([Oxenham and Simonson, 2006](#)). Recent data by [Eustaquio-Martin and Lopez-Poveda \(2011\)](#) show the opposite trend when using the TMC technique. The present NNTC data are consistent with [Eustaquio-Martin and Lopez-Poveda \(2011\)](#), in that filter sharpness increases with level in most subjects (Fig. 2).

The results of the present study and recent studies suggest that after controlling for off-frequency listening, PTCs and NNTCs may not be sensitive to the level-dependent shifts in BF or the broadening of tuning observed on the basilar membrane. In fact, in some instances, such as with NNTCs, the opposite trend is observed (filter bandwidths narrow with increasing level). In order to observe these level-dependent effects, behavioral data must be transformed by the cochlear I/O function at the signal place, as suggested by [Eustaquio-Martin and Lopez-Poveda \(2011\)](#). This transformation can be done using either the TMC technique ([Eustaquio-Martin and Lopez-Poveda, 2011](#)) or the GOM technique (present study). Both techniques assume that the off-frequency masker produces a linear response at the signal place. The validity of this assumption depends on the frequency of the masker being roughly an octave or more below the signal frequency. The off-frequency masker in [Eustaquio-Martin and Lopez-Poveda](#)

(2011) was 1.6 kHz ($0.4 * f_s$) whereas in the present study it was 2.5 kHz ($0.625 * f_s$). Despite using an off-frequency masker with a relatively higher frequency, there were no obvious violations of the assumption of linearity for the range of signal levels tested (30–60 dB SPL) in the present study. Evidence for this observation comes from the agreement between the derived I/O functions for the on-frequency masker and the signal [Fig. 5(A)]. Similarly, the iso-level filter bandwidths obtained were consistent with those reported by Eustaquio-Martin and Lopez-Poveda (2011), further suggesting the assumption of linearity may not have been violated for the 4 kHz signal used in the present study.

C. Deriving iso-level curves from PTCs and NNTCs

Iso-level filters from transformed PTCs and NNTCs are more consistent with physiological data compared to untransformed PTCs and NNTCs. As demonstrated by Eustaquio-Martin and Lopez-Poveda (2011), this consistency is the result of accounting for the influence of compression on masking thresholds. Thus, although iso-level filters and untransformed PTCs and NNTC come from the same data set, they produce very different estimates of frequency selectivity. In the current paper and in Eustaquio-Martin and Lopez-Poveda (2011), iso-level curves were derived using a large data set consisting of PTCs and NNTCs; however, it may be possible to directly measure iso-level filters. This measurement was proposed by Eustaquio-Martin and Lopez-Poveda (2011) as an extension of a technique developed by Moore and Glasberg (2003) and involves measuring gap thresholds for a fixed-level masker and signal as a function of masker frequency or notch width. The off-frequency TMC is then used as a linear reference to transform gap thresholds into output excitation. Such an approach seems appropriate for studies interested in measuring iso-level curves but not interested in comparing them to PTCs and NNTCs within the same data set. At low input levels, the cochlea acts as a linear system (e.g., Yates *et al.*, 1990). This suggests that bandwidths from low-level PTCs and NNTCs may be interpreted directly without requiring a transformation, provided that the signal is on the linear portion of the I/O function. Thus, the estimates of human frequency selectivity reported by Oxenham and Shera (2003) using the notched-noise method may be valid, given that they were obtained at a low signal level.

D. Using noise to restrict off-frequency listening

In this study and many previous studies (e.g., Johnson-Davies and Patterson, 1979; O'Loughlin and Moore, 1981; Nelson *et al.*, 1990; Oxenham and Plack, 1997), off-frequency listening was restricted by presenting a background noise simultaneously with the masker and signal. The presence of this background noise leads to a decrease in the masker level at threshold suggesting that the noise reduced the sensitivity to the signal. This reduction in sensitivity could be due to the noise masking auditory filters remote from the signal place (i.e., restricting off-frequency listening). Alternatively, the background noise could partially mask the signal by exciting the auditory filter centered at the signal place. If this were so,

the masking effect from the background noise and the masker would add. Such additivity of masking would also lead to a reduction in masker level at threshold. Finally, at high signal levels, presenting background noise may suppress the signal. In the case of a notched background noise, the response growth of the noise may be faster than that of the tonal signal due to compression. This results in a reduced effective SNR and may lead to suppression even though the spectrum level of the noise is appreciably lower than the level of the signal. It is possible that additivity of masking or suppression may account for the difference between basal and apical/restricted PTCs (Fig. 3). Despite this, there are reasonable arguments against these interpretations. For example, the cutoff frequencies for the low and high pass noise bands were 0.9 and $1.2f_s$, which corresponds to a notch width of 1200 Hz. As stated earlier, Q_{ERB} values at 4 kHz are around 15 in normal hearing listeners (Oxenham and Shera, 2003), which corresponds to a bandwidth of 266.67 Hz. This bandwidth is much narrower than the 1200 Hz notch width of the background noise. Thus, it seems unlikely that the background noise excited the auditory filter centered at the signal place and led to additivity of masking, at least at low signal levels. At higher signal levels, the auditory filter bandwidth would have to increase by a factor of 4.5 in order for the noise to excite the filter. This large increase in filter bandwidth is inconsistent with physiological data on the level-dependence of frequency tuning (see Ren and Nuttall, 2000). The difference between basal and basal/apical PTCs is unlikely to be explained by suppression because of the spectrum level selected for the background noise. This level was always 50 dB/Hz lower than the signal. Physiological data on two-tone suppression suggest that such a low level suppressor should have little effect on the basilar membrane response to the tone at CF (Ruggero, 1992). Overall, these arguments support the original assumption that the difference between basal and basal/apical PTCs was a result of off-frequency listening.

E. GOM with short maskers

Growth of off-frequency masking was used to estimate the cochlear I/O function. The estimates of cochlear compression obtained in the current study are within the range expected for normal hearing listeners. For example, Poling *et al.* (2012) estimated compression in a large group of normal and hearing impaired listeners using the TMC technique and found that compression estimates for *normal* hearing listeners ranged between 0.083 and 1.749 dB/dB. Several studies involving smaller groups of normal hearing listeners have reported compression estimates close to 0.2 (e.g., Oxenham and Plack, 1997; Yasin and Plack, 2003; Plack *et al.*, 2004). The estimates from the current study are higher than this value. The source of this discrepancy is uncertain; however, it may be related to the range of signal levels measured. Previous GOM studies with longer maskers were able to obtain threshold for signal levels as high as 75–90 dB SPL before reaching the maximum output for the masker (e.g., Oxenham and Plack, 1997; Nelson *et al.*, 2001; Yasin and Plack, 2005; Rosengard *et al.*, 2005). In contrast, in the current study with short maskers the highest signal level tested rarely exceeded 60 dB SPL before reaching the maximum

output for the masker. This suggests that the higher estimates of compression in the current study may be due to sampling a smaller range of the compressive portion of the cochlear I/O function. It is also possible these higher compression estimates may be related to the use of short maskers, which may control for gain reduction (e.g., Krull and Strickland, 2008; Jennings *et al.*, 2009; Roverud and Strickland, 2010).

F. Evaluating gain reduction with a precursor

Jennings *et al.* (2009) developed a forward-masking technique to measure the effects of gain reduction on frequency selectivity by presenting a fixed-level precursor prior to a short masker. A reduction in frequency selectivity was observed when the precursor was the same frequency as the signal. This suggests that the precursor approach (Krull and Strickland, 2008; Jennings *et al.*, 2009; Roverud and Strickland, 2010) may be more sensitive to evaluating the effects of gain reduction than simply manipulating masker duration (e.g., Kidd *et al.*, 1984; Bacon and Jesteadt, 1987; Plack and Arifanto, 2010). The effects of a precursor on estimates of frequency selectivity was evaluated in a related paper (Jennings and Strickland, 2012).

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APPENDIX: ROEX FILTER PARAMETERS FOR NNTC AND PTC DATA

The best fitting roex parameters and corresponding rms error values are presented in Tables I, II, and III for NNTCs, basal-restricted PTCs, and basal/apical-restricted PTCs, respectively.

TABLE I. Roex (pwtp) parameter estimates and rms error values for the NNTCs presented in Fig. 1.

Subject	L_p	pl	pu	t	$10 \cdot \log(w)$	rms error
1	40	35.8	87.0	3.0	-20.3	1.0
	45	131.9	41.3	8.6	-17.1	1.8
	50	199.9	77.2	13.6	-9.5	1.2
2	40	50.2	50.4	5.4	-33.6	3.3
	45	55.1	55.3	4.5	-28.7	1.7
	50	47.3	47.4	99.9	-38.0	3.3
3	55	115.4	122.9	58.6	-29.5	6.6×10^{-07}
	45	51.5	67.5	3.0	-16.0	2.0
	50	47.5	64.7	3.5	-16.5	1.7
	55	135.2	45.3	7.6	-13.6	0.7
4	60	17.8	17.9	3.8	-59.9	0.9
	45	38.6	87.1	4.3	-16.8	0.5
	50	197.6	65.1	14.3	-19.9	1.1
5	40	67.6	67.9	4.3	-19.8	1.8
	50	61.9	133.9	11.1	-23.2	0.5

TABLE II. Roex (pwtp) parameter estimates and rms error values for the basal-restricted PTCs presented in Fig. 3 (triangles).

Subject	L_p	pl	$10 \cdot \log$	tl	pu	rms error
1	35	43.802	-25.44	14.792	242.484	1.074
	40	40.543	-14.76	17.788	364.485	1.497
	45	20.114	-59.20	101.291	339.042	2.397
	50	51.735	-13.99	7.221	33.713	1.602
	55	55.667	-14.51	7.301	29.004	2.454
2	30	50.360	-30.39	10.770	126.133	4.088
	35	57.131	-28.45	8.978	146.870	1.319
	40	43.968	-17.65	11.925	139.971	1.017
	45	465.784	-9.32	13.033	47.390	1.760
	50	500.000	-6.91	12.669	49.971	1.608
3	55	3.573	-0.53	46.537	36.104	1.387
	45	499.991	-16.60	24.913	114.396	1.308
	50	40.171	-28.40	10.360	104.275	0.498
	55	73.491	-10.69	21.889	177.868	3.166
6	60	32.867	-25.83	1.000	46.209	1.974
	40	68.963	-38.71	9.735	102.723	2.591
	45	43.923	-28.77	2.737	37.630	1.508
	50	44.541	-30.49	1.995	38.024	2.707
	55	35.833	-39.20	1.009	28.131	1.829
	60	31.524	-7.95	1.709	185.362	2.4×10^{-06}

TABLE III. Roex (pwtp) parameter estimates and rms error values for the basal/apical-restricted PTCs presented in Fig. 3 (squares).

Subject	L_p	pl	$10 \cdot \log$	tl	pu	rms error
1	35	42.010	-25.31	14.397	267.480	0.672
	40	39.420	-17.05	17.042	227.496	0.826
	45	32.640	-31.47	1.000	342.185	0.965
	50	29.316	-28.02	1.000	275.210	1.773
	55	35.613	-33.24	1.000	306.211	1.574
2	30	48.168	-29.84	10.547	122.011	1.576
	35	41.629	-25.34	7.629	152.456	1.446
	40	41.145	-17.04	11.740	164.104	0.689
	45	43.236	-20.51	8.714	166.196	0.529
	50	40.435	-13.11	10.787	143.913	0.352
3	55	51.606	-14.39	5.984	90.620	0.526
	45	399.512	-19.52	24.913	93.772	2.636
	50	492.861	-15.22	28.947	115.375	2.648
	55	499.979	-17.13	23.662	104.195	2.313
6	60	106.918	-13.05	23.595	90.027	2.090
	40	68.963	-38.71	9.735	102.723	2.591
	45	66.535	-40.26	6.567	113.434	3.190
	50	425.878	-10.41	39.136	104.510	1.649
	55	438.884	-12.66	35.574	107.934	1.621
	60	137.258	-18.93	15.840	103.181	1.250

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