Research Article

Computational Modeling of Individual Differences in Behavioral Estimates of Cochlear Nonlinearities

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ABSTRACT

Temporal masking curves (TMCs) are often used to estimate cochlear compression in individuals with normal and impaired hearing. These estimates may yield a wide range of individual differences, even among subjects with similar quiet thresholds. This study used an auditory model to assess potential sources of variance in TMCs from 51 listeners in Poling et al. [*J Assoc Res Otolaryngol*, 13:91–108 (2012)]. These sources included threshold elevation, the contribution of outer and inner hair cell dysfunction to threshold elevation, compression of the off-frequency linear reference, and detection efficiency. Simulations suggest that detection efficiency is a primary factor contributing to individual differences in TMCs measured in normal-hearing subjects, while threshold elevation and the contribution of outer and inner hair cell dysfunction are primary factors in hearing-impaired subjects. Approximating the most compressive growth rate of the cochlear response from TMCs was achieved only in subjects with the highest detection efficiency. Simulations included off-frequency nonlinearity in basilar membrane and inner hair cell processing; however, this nonlinearity did not improve predictions, suggesting that other sources, such as the decay of masking and the strength of the medial olivocochlear reflex, may mimic off-frequency nonlinearity. Findings from this study suggest that sources of individual differences can play a strong role in behavioral estimates of compression, and these sources should be considered when using forward masking to study

cochlear function in individual listeners or across groups of listeners.

Keywords: masking, cochlear compression, individual differences, hearing loss, computational modeling

INTRODUCTION

Behavioral masking techniques can provide a non-invasive assessment of cochlear function in humans (for a review, see Oxenham and Bacon 2003; Plack 2005). Cochlear compression, characterized by the progressively slower rate (relative to unity) of basilar membrane response growth with increasing input level, is responsible for the large dynamic range in hearing and other perceptual effects (Oxenham and Bacon 2003). Behavioral measures often infer cochlear compression by estimating the cochlear input/output (*I/O*) function, which exhibits linear growth at low levels and compressive growth at mid to high levels (e.g., Ruggero and Rich 1991). Compression can be estimated from masking data by calculating the minimum slope of the derived *I/O* function (Yasin and Plack 2005) or by fitting a linear function to the data above the breakpoint that separates the linear and compressive regions (Yasin and Plack 2003). Temporal masking curves (TMCs) have gained acceptance as a behavioral measure for estimating cochlear compression in adults with normal and impaired hearing (Nelson et al. 2001). In TMCs, masking thresholds are obtained as a function of the temporal

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interval between the masker and probe (i.e., probe delay), for a probe whose level is slightly above the listener's threshold (~ 10 dB sensation level [SL]) and for masker frequencies at (on-frequency) or roughly one octave below (off-frequency) the probe frequency. Compression is estimated from TMCs by plotting the off-frequency thresholds as a function of the on-frequency thresholds and fitting these data with a function, from which the slope is calculated. This procedure for estimating compression is based on several assumptions (Wojtczak and Oxenham 2009, 2010) including the notion that the off-frequency masker grows linearly through an auditory filter whose characteristic frequency (CF) is centered on the probe frequency (providing a "linear reference"), and post-cochlear processes are cancelled in the comparison with the on-frequency masker data. For normal-hearing listeners, off-frequency TMCs measured with a 1-kHz probe (or higher) exhibit shallow growth and have relatively high thresholds. Conversely, when the masker is on-frequency, thresholds often increase rapidly, and the slope is greatest for mid-range probe delays (Nelson et al. 2001). Compression estimated from TMCs typically ranges between 0.01 and 0.56 dB/dB (Rosengard et al. 2005). Compared to individuals with normal hearing, hearing-impaired listeners typically exhibit (1) higher on- and off-frequency masking thresholds, (2) a slightly shallower off-frequency TMC slope, and (3) an appreciably shallower on-frequency TMC slope, when the probe is at the same SL as the normal-hearing listeners. These differences may lead to estimates that suggest less compression (i.e., more linear growth), although large individual differences in compression estimates exist (Plack et al. 2004).

One limitation of using TMCs to estimate compression is the substantial individual differences among adults with similar normal or elevated detection thresholds. As discussed by Poling et al. (2012), sources of individual differences among listeners with similar and different thresholds may include (1) the degree of hearing loss, (2) the contribution of outer (OHC) and inner (IHC) hair cell dysfunction to the hearing loss, (3) the degree of cochlear nonlinearity (i.e., compression), (4) the influence of the medial olivocochlear (MOC) reflex, (5) the ability to make use of stimulus cues for detecting the probe (i.e., detection efficiency), (6) the ratio of frequencies for on- and off-frequency maskers (i.e., the linear reference), (7) durations of the masker and probe (e.g., Lopez-Poveda et al. 2003), (8) learning/practice effects, and (9) methods for fitting/deriving compression. Some of the proposed sources of individual differences in compression estimates originate in a violation of the assumptions made when interpreting TMCs (Wojtczak and Oxenham 2009, 2010). For example, the growth of the off-frequency

masker may be compressive through the auditory filter whose CF is centered on the probe frequency, resulting in steeper slopes (less compression) of the inferred I/O function (Lopez-Poveda and Alves-Pinto 2008; Plack and Arifanto 2010). The amount of this "off-frequency" compression may vary among listeners and contribute to individual differences in compression estimates. In addition, Wojtczak and Oxenham (2009) suggested that stimulation of the MOC reflex may violate the assumption that post-cochlear processes exert equal influence on both on- and off-frequency TMCs. To the extent that MOC reflex strength varies within an otherwise homogeneous group (e.g., Maison and Liberman 2000), this reflex may serve as a source of variance in compression estimates from TMCs.

In hearing-impaired adults, individual differences in TMCs may result from different degrees of hearing loss (Nelson et al. 2001; Plack et al. 2004; Rosengard et al. 2005) and the contribution of OHC and IHC dysfunction to the hearing loss (e.g., Howgate and Plack 2011). With hearing loss, masker levels at threshold are higher and often exhibit smaller differences between on- and off-frequency maskers, particularly at short masker-probe delays. This pattern may be explained by dysfunctional OHCs, resulting in less cochlear gain at the probe frequency, which decreases sensitivity to on-frequency signals more than off-frequency signals. In contrast, some degree of IHC dysfunction is suspected if the difference between on- and off-frequency TMCs at small probe delays remains large (Howgate and Plack 2011).

Another source of individual differences in TMCs may relate to the ability of the listener to use cues important for detecting the probe (i.e., "detection efficiency"). In masking tasks, the probe may be distinguished from the masker on the basis of several cues (i.e., temporal, frequency, and/or level cues), and listeners may differ in their ability to identify and exploit these cues. Detection efficiency may explain superior performance in masking tasks for musicians than non-musicians (Fine and Moore 1993; Oxenham et al. 2003; Bidelman et al. 2014), adults than children (Hill et al. 2004), and in individuals without than with dyslexia or language impairments (Hartley and Moore 2002). Studies suggest that detection efficiency in normal-hearing listeners is primarily influenced by factors central to cochlear processing including memory, attention, and experience (Patterson et al. 1982; Werner and Bargones 1991). Detection efficiency is a standard component of techniques used to estimate frequency selectivity from masking thresholds (Patterson and Nimmo-Smith 1980; Patterson et al. 1982) and is often modeled as the degree to which probe power must exceed masker power (in dB) through an auditory filter at detection threshold (i.e., the signal-to-masker ratio or SMR). Detection efficien-

cy can vary appreciably among normal-hearing listeners (Patterson 1976; Leek and Summers 1993) and accounts for individual differences in estimates of frequency resolution, suggesting that it may be a source of individual differences in TMCs. In hearing-impaired individuals, poor detection efficiency (i.e., higher SMRs) may result from (1) a lack of efficiency in the central auditory nervous system, (2) a degraded signal from which the detector cannot extract the relevant cues, or (3) some combination of both.

This study aimed to identify the primary sources of individual differences in TMCs in a large dataset of adults with normal and impaired hearing (Poling et al. 2012) by predicting TMCs with a computational model of the auditory periphery (Zilany et al. 2009). This model, when expanded to include the processes of temporal integration and detection, is effective at predicting masking thresholds (Jennings and Strickland 2012) and is capable of simulating effects of hearing loss, the contribution of OHC and IHC dysfunction, nonlinearity of the off-frequency reference, and detection efficiency. This modeling approach allows each potential source of individual differences to be evaluated in a relatively independent manner, revealing how these sources influence TMCs and estimates of compression.

METHODS

TMCs were predicted using techniques similar to those of Plack et al. (2002) and Jennings and Strickland (2012). These techniques involved simulating peripheral processes (i.e., middle and inner ear signal processing), temporal integration, and detection. The peripheral auditory system was simulated using the computational model described by Zilany et al. (2009), which is based on physiological responses from cats and accounts for middle ear transmission (Bruce et al. 2003) and cochlear processing (Heinz et al. 2001; Zhang et al. 2001; Zilany and Bruce 2006, 2007), including the effects of cochlear compression, suppression, level-dependent tuning, and the contribution of OHC and IHC dysfunction. Temporal integration and detection were simulated using a temporal window model (Oxenham and Moore 1994), which has been effective in predicting behavioral thresholds in forward masking (Oxenham and Bacon 2003). The simplicity of the temporal window model fits well with the scope of the current study; however, other models of central processing (e.g., modulation filter bank models (Jepsen and Dau 2011)) will likely produce similar results and may be more physiologically realistic (Nelson et al. 2009).

Subjects

As described in Poling et al. (2012), 51 subjects were divided into low ($n=24$; S1–S24; mean age=39.6 years; probe thresholds 13.2–22.2 dB SPL), mid ($n=11$; S25–S35; mean age=59.3 years; probe thresholds 23.9–34.2 dB SPL), and high ($n=16$; S36–S51; mean age=76.1 years; probe thresholds 41.0–57.7 dB SPL) threshold groups based on thresholds for the 20-ms, 1-kHz probe.

Stimuli

The stimuli presented to the model were the same as those in Poling et al. (2012), except the probe frequency (f_p) was 3 kHz instead of 1 kHz to account for the difference between cat and human cochlear frequency maps (Greenwood 1990). Briefly, the on-frequency sinusoidal masker and the sinusoidal probe were 3 kHz. The frequency of the off-frequency masker was a model parameter (see “Procedures” section). Masker and probe durations were 200 and 20 ms, respectively, including 10-ms rise/fall ramps. The interval between the offset of the masker and the onset of the probe (i.e., the probe delay) ranged from 0 to 70 ms, in 10-ms steps. The probe level was set to 10 dB SL, where absolute threshold was defined as the probe level needed to produce an electrical potential of 5.1×10^{-5} V in the model’s IHC module. This value is produced when a 0-dB SPL, 3-kHz tone is presented to the model with OHCs and IHCs fully functional (i.e., normal-hearing model) and was chosen to approximate quiet thresholds at 1 kHz in adults with normal hearing.

Procedures

TMC thresholds were predicted for each subject by comparing simulations with the probe (masker+probe simulation) and without the probe (masker simulation) and calculating the SMR for an array of masker levels, ranging from 0 to 120 dB SPL in 5-dB steps. For each combination of masker level, masker frequency, and probe delay, the IHC response of the model CF centered on the probe frequency was squared and convolved with a windowing function to simulate temporal integration (Fig. 1). This resulted in a time-varying output from which the dB difference between masker and masker+probe simulations was calculated. The largest dB difference across time was defined as the SMR for a given masker level, masker frequency, and probe delay. Additional normal-hearing simulations (not shown) covered a range of model CFs above and below the probe frequency and revealed that the model CF centered on the probe frequency always produced the best SMR. This suggests that off-frequency listening was unlikely; therefore, only the

FIG. 1. Block diagram of components of the model used for simulating temporal masking curves. Stimuli are processed by the peripheral model, resulting in a time-varying inner hair cell (IHC) response. This response is squared and convolved with a windowing function (temporal window). Comparing masker simulations (dashed

lines) with masker+probe simulation (solid lines) results in a masker–probe ratio (box labeled SMR and predictor k [see text]). An elevation in threshold and the contribution of outer and inner hair cell dysfunction was simulated using parameters C_{OHC} and C_{IHC} .

model CF centered on the probe frequency was used to simulate TMCs in this experiment. This finding is consistent with TMCs being measured with a low probe level, where spread of excitation is minimal (Nelson et al. 2001). The IHC response was used as the input to the temporal window model because it includes nonlinear processing associated with the basilar membrane and the IHC receptor potential, both of which are thought to play a role in interpreting TMCs (Lopez-Poveda et al. 2003; Plack and Arifanto 2010). As with many previous studies using the temporal window model (Oxenham 2001; Plack et al. 2002; Jennings and Strickland 2012), processing associated with the auditory nerve (e.g., synaptic responses, firing rate saturation) was not simulated. Because the IHC response is deterministic (as are the sinusoidal stimuli), only one presentation for each simulation type (i.e., masker simulation or masker+probe simulation) was needed to obtain the IHC response.

After SMRs had been obtained for all masker levels (for a given probe delay and masker frequency), threshold was interpolated to find the masker level corresponding to a criterion SMR. This ratio (denoted k) was applied to all predicted thresholds of a given subject and can be interpreted as the efficiency with which the probe is detected, where high ratios correspond to poor efficiency. The temporal integration window consisted of a weighted sum of two exponentials (see Oxenham and Moore 1994), where the time constants (τ_1 , τ_2) of these exponentials and

the weighting factor (ω) were set according to Oxenham (2001): $\tau_1=4.6$ ms, $\tau_2=16.6$ ms, and $\omega=0.17$.

Four predictors were used to simulate TMCs. Each predictor had 13 possible values and spanned an appropriate numerical range based on the presumed physiological properties of the predictor or the use of the predictor in previous studies. The first predictor was threshold elevation (), which ranged from 0 to 60 dB in 5-dB steps and was simulated by adjusting the amount of OHC and IHC dysfunction (C_{OHC} and C_{IHC} in Fig. 1) at the CF centered on the probe frequency. The 0-to-60-dB range corresponds well with the range of probe detection thresholds for the subjects in Poling et al. (2012). This elevation in threshold was the result of a mixture of OHC and IHC dysfunction, simulated as the proportion of the hearing loss due to OHCs (p_{OHC} , second predictor) and ranging from 0 to 1 in 0.0833 steps. The degree of cochlear nonlinearity (i.e., gain and compression) depended on the status of θ and p_{OHC} and was not adjusted as an independent predictor. Thus, if the data of two given listeners were fit with the same θ and p_{OHC} , the model predicted these listeners to have the same cochlear I/O function. The third predictor was detection efficiency (k , box labeled “SMR” in Fig. 1), which was modeled as a constant SMR at the output of the integration window for all predicted thresholds of a given subject (Oxenham and Moore 1994). k ranged from 0.1 to 8 in logarithmically spaced steps, which is consistent with the range and distribution of k

reported in previous studies using the temporal window model (e.g., Plack and Oxenham 1998; Oxenham and Plack 2000; Plack and Drga 2003). The final predictor was the frequency of the off-frequency masker (f_m), which indirectly simulated a change in the slope of the linear reference by applying more active processing to the off-frequency masker. The Zilany et al. (2009) model does not allow the user to directly change the response growth of an off-frequency stimulus; however, due to basilar membrane mechanics, the response growth can be indirectly simulated with a change in stimulus frequency. As the off-frequency masker approaches 3 kHz, its response growth at the 3-kHz place will become progressively more compressive. Simulating a change in the slope of the off-frequency reference by changing f_m will result in a change in slope and a change in the gain (i.e., intercept) applied to the off-frequency masker. This approach may be more realistic than changing only the slope of the off-frequency reference, given that compression and gain are expected to vary together as they both originate from the active process. Off-frequency maskers ranged between 0.58 (2.0 kHz) to 1.58 (1.0 kHz) octaves below the simulated probe frequency (3.0 kHz) in 0.083-kHz steps. This range of masker frequencies corresponds to an off-frequency response growth between 0.65 and 1.1 dB/dB.

Predictors were allowed to vary to minimize the root mean square (rms) error between measured and predicted TMCs for each subject in order to determine the best-fitting predictors. Model simulations resulted in 28,561 TMC templates (four predictors with 13 potential values per predictor; $13^4=28,561$), and the rms error was calculated from each of these TMC templates.

RESULTS AND DISCUSSION

Model simulations effectively predicted the mean on- and off-frequency TMCs for the low, mid, and high threshold groups (Fig. 2) where the rms error was 2.97, 2.47, and 1.66 dB, respectively. As indicated by the large standard deviations in Figure 2, substantial individual differences exist; therefore, predicting on- and off-frequency TMCs for each subject provides a more rigorous evaluation of the model.

Differences between measured and predicted on- and off-frequency TMCs for each individual subject were relatively small; mean rms error was 4.75 dB ($\sigma=1.6$ dB; range=2.0–8.1 dB), 2.99 dB ($\sigma=1.1$ dB; range=1.31–4.86 dB), and 3.19 dB ($\sigma=1.87$ dB, range=1.8–8.8 dB) for the low, mid, and high threshold groups, respectively. Tables 1 (low threshold

FIG. 2. Mean temporal masking curves measured using on-frequency maskers (open symbols) and off-frequency maskers (solid symbols) for subjects in the low, mid, and high threshold groups (panels). Dotted and solid lines are model fits to the mean data. Error bars are one standard deviation about the mean.

group) and 2 (mid and high threshold groups) present the best-fitting predictors and rms error for each subject. Many combinations of predictors, in addition to the best-fitting predictors, produced similarly low rms errors (see the Appendix for a description of how rms error varied across changes in predictors). The final three columns in Tables 1 and 2 display quantities for an analysis that will be discussed in “Sensitivity to k ”. Figures 3 and 4 display TMCs (symbols) and model predictions (lines) for the low threshold group (Fig. 3) and mid and high threshold groups (Fig. 4).

Parameter Sensitivity Analysis

A parameter sensitivity analysis was performed using methods similar to those of Cotter (1979) and Cook et al. (2009) to determine which predictors were most

TABLE 1

Parameter values from the best-fitting model simulations and probe thresholds, temporal integration and the input signal-to-masker ratio for subjects in the low threshold group

<i>S</i>	θ	<i>k</i>	f_m	p_{OHC}	<i>rms</i>	<i>PT</i>	<i>TI</i>	<i>ISMR</i>
S1	0	0.10	1.42	0	7.24	13.2	12.4	60.3
S2	0	1.56	1.00	0	4.14	13.4	8.8	49.3
S3	0	2.14	1.25	0	3.27	13.8	12.0	44.4
S4	0	0.65	1.75	0	3.76	13.9	5.4	41.6
S5	5	1.07	1.33	0	4.16	15.0	–	51.1
S6	0	0.65	1.50	0	2.07	15.3	9.8	41.3
S7	0	0.65	1.25	0	2.42	15.7	4.0	50.4
S8	10	1.07	1.75	0	5.86	15.9	10.1	46.3
S9	0	0.65	1.00	0	6.86	16.0	9.2	48.5
S10	0	0.10	1.17	0	4.50	16.6	17.4	55.8
S11	5	2.14	1.08	0	4.98	17.5	–	43.2
S12	0	0.33	2.00	0	4.22	17.5	13.1	35.3
S13	0	0.33	1.17	0	3.21	17.8	11.1	49.5
S14	5	0.65	1.08	16.66	4.09	18.2	7.1	53.7
S15	5	2.14	1.08	0	5.45	18.2	10.7	46.5
S16	5	1.07	1.25	0	3.74	18.4	15.3	46.4
S17	10	1.07	1.67	0	3.65	19.2	–	47.9
S18	15	1.56	2.00	0	8.11	19.5	11.9	43.8
S19	10	0.33	1.25	41.65	4.35	19.7	11.9	51.4
S20	0	0.33	1.00	0	6.17	19.7	16.8	50.0
S21	0	0.33	1.42	0	4.94	20.9	9.4	44.3
S22	5	0.33	1.08	0	7.79	21.2	13.7	46.6
S23	10	1.07	1.75	8.33	3.62	21.4	11.1	43.0
S24	10	5.11	1.00	0	5.41	22.2	7.4	43.8
Min	0	0.10	1.00	0.00	2.07	13.2	4.0	35.3
Max	15	5.11	2.00	41.65	8.11	22.2	17.4	60.3
Mean	1.25	1.06	1.34	2.78	4.75	17.51	10.88	47.26

S subject, θ threshold elevation, re: 0 dB SPL, *k* detection efficiency, f_m frequency of the off-frequency masker in kHz, p_{OHC} proportion of outer hair cell dysfunction, *rms* root mean square error, *PT* probe thresholds, *TI* temporal integration, *ISMR* input signal-to-masker ratio

effective at reducing the rms error between measured and predicted TMCs. This analysis involved observing the increase in rms error produced when a given predictor was held constant, while other predictors varied. Sensitivity analyses were divided into normal hearing (low threshold group) and hearing-impaired (mid and high-threshold groups) analyses and further divided into on- and off-frequency TMC analyses. Performing separate analyses allowed the predictors and f_m to be evaluated on data sets where they are expected to play a role (i.e., on hearing-impaired subjects [θ] and on the off-frequency data [f_m]). For all sensitivity analyses, predictors were held constant at their median values. The results of the parameter sensitivity analysis are shown in Figures 5 (normal-hearing subjects) and 6 (hearing-impaired subjects), where the distribution of rms error is compared between the original minimization procedure ("vary all") and simulations where a predictor was held constant ("fix pred."). Analyses are shown for the on-frequency data (A), off-frequency data (B), and combined on- and off-frequency data (C).

Model simulations for the normal-hearing subjects were most sensitive to *k* and f_m and less sensitive to θ

and p_{OHC} (Fig. 5C). Sensitivity to *k* in normal-hearing simulations was also reported by Oxenham and Moore (1994) who used the temporal window model to simulate the additivity of forward masking (e.g., Humes and Jesteadt 1989). The relative insensitivity to θ and p_{OHC} was expected given that these parameters simulated aspects of hearing loss. Despite this, a small increase in rms error was observed when θ was held constant, suggesting that differences in hearing thresholds within the normal range contribute to individual differences in TMCs measured in normal-hearing subjects. Simulations of TMCs from hearing-impaired subjects were sensitive to all predictors, but particularly sensitive to p_{OHC} and θ (Fig. 6C). This suggests that the major sources of variance in predicting TMCs from hearing-impaired subjects are the degree of hearing loss (θ) and the contribution of OHCs to the hearing loss (p_{OHC}).

Sensitivity to *k*

On- and off-frequency TMCs in inefficient listeners (high *k*; e.g., S3, S30, S40) were generally shallower and had lower masking thresholds than efficient

TABLE 2

Parameter values from the best-fitting model simulations and probe thresholds, temporal integration and the input signal-to-masker ratio for subjects in the mid and high-threshold groups

<i>S</i>	θ	<i>k</i>	f_m	p_{OHC}	<i>rms</i>	<i>PT</i>	<i>TI</i>	<i>ISMR</i>
S25	20	4.27	1.92	0.00	4.86	23.9	16.0	39.2
S26	25	6.98	1.67	0.00	3.40	26.0	8.4	40.3
S27	20	1.56	1.17	0.00	2.91	26.0	–	55.3
S28	20	4.27	1.75	0.00	3.69	27.2	7.4	33.4
S29	15	2.14	2.00	91.63	2.60	27.8	9.1	20.6
S30	25	8.00	1.25	24.99	1.67	28.4	7.6	35.8
S31	15	0.10	1.00	58.31	4.31	28.6	14.6	62.6
S32	15	0.33	1.08	91.63	2.28	28.6	9.9	40.2
S33	15	0.33	1.17	91.63	2.77	29.8	13.5	39.4
S34	30	6.01	1.83	16.66	1.31	31.2	9.9	34.1
S35	30	3.49	1.42	58.31	3.09	34.2	6.7	31.2
S36	30	0.65	1.67	74.97	2.74	41.0	8.5	24.6
S37	35	8.00	1.92	33.32	3.64	43.0	2.8	16.8
S38	30	1.56	1.75	58.31	2.65	43.2	9.7	22.8
S39	45	8.00	1.08	66.64	2.46	45.3	4.4	23.5
S40	45	8.00	1.00	66.64	1.94	45.6	5.6	21.9
S41	45	5.11	1.00	74.97	2.11	46.0	1.7	26.1
S42	40	6.98	1.00	66.64	2.52	47.0	3.9	19.8
S43	30	0.65	1.17	66.64	1.61	47.5	6.4	33.1
S44	35	1.56	1.00	66.64	3.28	47.7	7.3	37.0
S45	25	0.33	1.00	66.64	8.77	51.5	8.4	38.1
S46	45	2.14	1.00	66.64	3.03	53.4	8.3	27.0
S47	35	0.33	1.00	49.98	2.32	53.9	8.9	40.4
S48	45	3.49	1.00	74.97	2.23	54.1	4.1	20.2
S49	30	0.10	1.00	83.30	6.30	55.7	7.0	29.5
S50	45	1.07	1.00	91.63	1.59	57.2	7.2	12.6
S51	40	5.11	1.00	58.31	3.81	57.7	8.2	19.8
Min	15	0.10	1.00	0.00	1.31	23.9	1.7	12.6
Max	45	8.00	2.00	91.63	8.77	57.7	16.0	62.6
Mean	30.74	3.35	1.29	55.53	3.11	40.79	7.907	31.31

S subject, θ threshold elevation, re: 0 dB SPL, *k* detection efficiency, f_m the frequency of the off-frequency masker in kHz, p_{OHC} proportion of outer hair cell dysfunction, *rms* root mean square error, *PT* probe thresholds, *TI* temporal integration, *ISMR* input signal-to-masker ratio

listeners (see Figs. 3 and 4, and Tables 1 and 2). These findings suggest that detection efficiency may influence compression estimates by restricting the range of levels over which the cochlear *I/O* function is sampled. Specifically, the cochlear *I/O* functions of inefficient listeners were sampled over a relatively narrower range than efficient listeners; this finding is best illustrated in the low threshold group. Figure 7 displays the derived *I/O* function of an efficient listener (S1, left) and an inefficient listener (S3, right). The *I/O* function (Fig. 7, solid black lines) derived from the TMCs of inefficient listeners span below and possibly slightly above the compression breakpoint (i.e., the transition between linear and compressive growth of the expected cochlear *I/O* function (gray lines) obtained directly from the model). This suggests that compression derived from these listeners was equivalent to a “local” compression rather than the “maximal” compression. In this context, local compression is the minimum slope of a small segment of the cochlear *I/O* function (e.g., 20–40 dB SPL), while maximal compression is the minimum slope across the entire input dynamic range

(i.e., 0–120 dB SPL). An estimate of local compression is a concern, considering the implicit assumption that behavioral measurements approximate the maximal compression. S1 and other efficient listeners had steep on-frequency TMCs and a wide sample of input levels to derive *I/O* functions, many of which were above the compression breakpoint, suggesting that these data may more accurately approximate maximal compression (Fig. 7, left). Measuring TMCs over a broader range of probe delays or customizing the range of probe delays used for each subject may avoid narrowly sampling the cochlear *I/O* function in inefficient listeners. A challenge to measuring longer probe delays is the potentially high masker levels in the off-frequency TMC, which may exceed the limits of the experimental equipment or the listener’s loudness discomfort level. These limitations may affect the ability to obtain pairs of on- and off-frequency thresholds needed to infer the cochlear *I/O* function. Extrapolation (e.g., Lopez-Poveda et al. 2003) or a technique that does not require an off-frequency masker (e.g., Plack and O Hanlon 2003; Yasin et al.

FIG. 3. Temporal masking curves for individual subjects in the low threshold group. Symbols and lines are as in Figure 2.

2013) may be reasonable alternatives to avoid these high levels.

The simulations allowed k to vary among subjects, which explicitly assumes that individual differences among listeners are partially due to differences in efficiency. Despite this, the interpretation of k may not be straightforward. For example, k could be interpreted as an ad hoc adjustment to predicted thresholds, given that it assumes the last position in the model architecture. Correlation analyses were performed to test whether k can be interpreted as truly representing differences in detection efficiency among listeners. These analyses were based on the assumptions that (1) efficiency is a central process (e.g., Patterson et al. 1982; Werner and Bargones 1991) and (2) certain behavioral measurements

FIG. 4. Temporal masking curves for individual subjects in the mid and high threshold groups. Symbols and lines are as in Figure 2.

should vary with k if such measurements are minimally influenced by peripheral nonlinearities. To test these assumptions, two behavioral measurements were evaluated: (1) temporal integration and (2) the “input SMR” for the off-frequency masker at 0-ms delay (i.e., a form of critical ratio; Hawkins and Stevens (1950)). These measurements are displayed in Tables 1 and 2 in the columns labeled “TI” and “ISMR,” respectively.

Temporal integration was calculated from the behavioral data as the difference between quiet thresholds for a 20-ms, 1-kHz tone (i.e., the probe) and a 200-ms, 1-kHz tone. These thresholds were obtained from the dataset of Poling et al. (2012). Although the model’s power integration of the post-cochlear stimulus (i.e., temporal window) predicts

FIG. 5. Parameter sensitivity analysis for temporal masking curve simulations of subjects in the low threshold group. The distributions of rms error values are plotted for simulations where all parameters varied (*solid lines*) or one parameter was held constant (*dashed lines*). Parameters were detection efficiency (k), off-frequency masker frequency (f_m), the proportion of OHC dysfunction (p_{OHC}), and quiet threshold for the probe (θ). **A** Parameter sensitivity analysis of the on-frequency TMCs. **B** Parameter sensitivity analysis of the off-frequency TMCs. **C** Parameter sensitivity analysis of the combined on- and off-frequency TMCs.

lower thresholds for the longer tone, this improvement may be realized by another mechanism, such as multiple looks (Viemeister and Wakefield 1991). Multiple looks theory assumes that quiet thresholds improve with probe duration because listeners have more “looks” at the probe. Listeners presumably combine these looks and thereby increase the probability of detecting the probe. The efficiency of this multiple looks mechanism may vary among subjects. Temporal integration is thought to occur in the central auditory nervous system (Zwislocki 1960) and is independent of peripheral nonlinearity when measured near absolute threshold (Plack and Skeels 2007). These findings and the observation that temporal integration varies substantially among individuals with similar thresholds (e.g., Florentine et al. 1988) support the assumption that temporal integration may be correlated with k . The “input SMR” was calculated as the difference in level at threshold between the probe and off-frequency masker, for the shortest probe delay (i.e., 0 ms). This masking threshold was chosen to avoid cochlear nonlinearity, provided that signals one octave below the CF exhibit linear growth (Yates et al. 1990; Ruggero et al. 1997). Given that k was modeled as the output SMR, it seems

FIG. 6. Parameter sensitivity analysis for temporal masking curve simulations of subjects in the mid and high threshold groups. The distributions of rms error values are plotted for simulations where all parameters varied (*solid lines*) or one parameter was held constant (*dashed lines*). Parameters were detection efficiency (k), off-frequency masker frequency (f_m), the proportion of OHC dysfunction (p_{OHC}), and quiet threshold for the probe (θ). **A** Parameter sensitivity analysis of the on-frequency TMCs. **B** Parameter sensitivity analysis of the off-frequency TMCs. **C** Parameter sensitivity analysis of the combined on- and off-frequency TMCs.

reasonable that the input SMR would be strongly correlated under conditions where cochlear nonlinearity is minimized. If the input SMR is processed linearly (i.e., conditions with an off-frequency masker), the only difference between k and the input SMR would be the decay of masking. Thus, k and the input SMR should be correlated if k truly reflects detection efficiency.

Correlations were calculated to assess relationships between k and subject age, measured probe threshold, temporal integration, and the

FIG. 7. Derived input/output (I/O) functions in an efficient (*left*) and inefficient (*right*) listener. Symbols are the derived I/O functions from TMC data (I/O_{obs}). The gray lines are the expected I/O functions from the model, which were shifted vertically to align with I/O_{obs} .

FIG. 8. Scatterplots of model parameters and behavioral thresholds or metrics of efficiency. Squares, triangles, and diamonds correspond to the low, mid, and high threshold groups, respectively. **A** Scatterplot of quiet thresholds and threshold elevation (θ). **B** Scatterplot of temporal integration (difference in quiet threshold between a 20-ms, 1-kHz tone and a 200-ms, 1-kHz tone) and a logarithmic transform of detection efficiency (k). The logarithmic transform was used to normalize the variance of k . **C** Scatterplot of the input SMR and $\log_{10}k$. The input SMR is the difference in level at threshold between the probe and off-frequency masker, for the shortest probe delay (i.e., 0 ms). **D** Scatterplot of the slope of the off-frequency TMC and the model's f_m predictor (see text) for subjects in the low threshold group.

input SMR. A significant positive correlation ($r^2=0.85$; $p<0.001$; Fig. 8A) was observed between measured detection thresholds for the 1-kHz probe and the best-fitting threshold elevation. This suggests that the model was accurate at accounting for the distribution of thresholds observed among the listeners. Correlations (not shown) between k and age ($r^2=0.26$; $p>0.05$) or measured quiet thresholds at 1 kHz ($r^2=0.02$; $p>0.05$) were not statistically significant after controlling for collinearity among age and quiet thresholds at 1 kHz. A weak-to-moderate negative correlation ($r^2=0.27$; $p<0.001$; Fig. 8B) was observed between k and temporal integration, suggesting that temporal integration increases as k decreases (i.e., better efficiency). Finally, a moderate negative correlation ($r^2=0.31$; $p<0.001$; Fig. 8C) was found between k and the input SMR. The correlations between k and temporal integration or the input SMR are consistent with the assumption that k can be interpreted as detection efficiency. For subjects in the mid and high threshold groups, poor detection efficiency does not necessarily indicate a deficit of the central auditory system but may suggest a peripheral degradation of important cues that cannot be resolved by the central detector. The degree to which detection efficiency is compromised by peripheral degradation of detection cues is unknown, as are the sources of this degradation; however, these sources may be related to poorer frequency resolution (e.g., Sellick et al. 1982) or altered neural adaptation (Scheidt et al. 2010). Peripheral degradation of detection cues may also contribute to increased individual differences among hearing-impaired listeners, as compared to normal-hearing listeners, in TMCs and other psychophysical and speech perception tasks (e.g., Moore 2007).

The correlation between the input SMR and k suggests that inefficient listeners, in a masking experiment with a given probe frequency, can be identified (with some degree of accuracy) by measuring the input SMR. The ability to identify and group efficient and inefficient listeners may serve as a method for accounting for extraneous sources of variance when analyzing data from masking experiments. The variance in the input SMR not accounted for by k may originate in mechanisms not included in the model's architecture, such as the MOC reflex (Krull and Strickland 2008; Jennings et al. 2009; Wojtczak and Oxenham 2009; Roverud and Strickland 2010; Wojtczak and Oxenham 2010; Aguilar et al. 2013). However, the current lack of an independent measure of MOC reflex strength in humans prevents a quantitative assessment of the variance accounted for by this potential factor. Similarly, variance in the input SMR not accounted for by k may also stem from the use of a fixed temporal integrator in all predictions.

FIG. 9. rms error (dB) of model predictions considering only the on-frequency (wide light blue bars) or off-frequency (narrow black bars) temporal masking curves in subjects in the low, mid, and high threshold group.

Sensitivity to f_m

The slopes of off-frequency TMCs are shallower in hearing-impaired listeners than in normal-hearing listeners (e.g., Plack et al. 2004). This finding may be evidence for off-frequency nonlinearity in normal-hearing listeners (Lopez-Poveda et al. 2005; Rosengard et al. 2005). Off-frequency nonlinearity may emerge from active basilar membrane mechanics or from the saturating nonlinearity of the IHC receptor potential (Lopez-Poveda et al. 2003; Plack and Arifanto 2010). The degree of active processing applied to the off-frequency masker was simulated by adjusting the frequency of the off-frequency masker (f_m), where maskers closer to the probe frequency had greater nonlinearity through the model CF centered on the probe frequency. Adjusting f_m resulted in a change in the slope and intercept of the predicted off-frequency TMC, where higher-frequency off-frequency maskers had steeper slopes and lower intercepts.

Plack et al. (2004) reported off-frequency TMC slopes of 0.2–0.5 dB/ms for the majority of their hearing-impaired listeners, suggesting that steeper slopes may indicate off-frequency nonlinearity. Eight subjects in the low threshold group (i.e., S9, S10, S11, S15, S19, S20, S22, S24) and three in the mid and high threshold groups (i.e., S32, S37, S49) had off-frequency TMC slopes greater than 0.5 dB/ms. For these 11 subjects, adjusting f_m improved model predictions; however, this adjustment was often toward relatively lower f_m , which resulted in *shallower* rather than steeper predicted off-frequency TMCs.

This finding is apparent in the strong negative correlation between f_m and the slope of the behavioral off-frequency TMC in the low threshold group (Fig. 8D). Further analysis (not shown) revealed that increasing f_m (i.e., toward greater active processing) resulted in steeper predicted off-frequency TMCs; however, these TMCs had much lower thresholds than the behavioral off-frequency TMCs and thus high rms error. This suggests that the model's sensitivity to f_m is due to this predictor's ability to shift the off-frequency TMC toward higher or lower thresholds rather than change the slope. In physiological terms, this suggests that f_m served more to adjust the gain or frequency selectivity of a given subject rather than the degree of off-frequency nonlinearity. Psychoacoustic (Oxenham and Shera 2003) and otoacoustic emission (Shera et al. 2002; Shera and Guinan 2003) studies suggest that humans may have sharper frequency selectivity than laboratory animals (however, see Ruggero and Temchin (2005), and Lopez-Poveda and Eustaquio-Martin (2013)). The Zilany et al. (2009) model is based on cat physiology; therefore, the model's frequency resolution may be broader than that of human subjects.

The results of the simulations suggest that the steep off-frequency TMC observed in some subjects was unlikely due to active basilar membrane mechanics applied to the off-frequency masker. When simulating greater active processing, the model predicts that the relatively greater gain will result in a more effective off-frequency masker (contrary to the behavioral data), and to an increased off-frequency

TMC slope. Although model simulations included nonlinearity from the IHC receptor potential, it appears that IHC nonlinearity was insufficient to account for the steep slopes of the behavioral off-frequency TMCs. The IHC module of the Zilany et al. (2009) model was originally developed based on physiological data in cat (Dallos 1985; Palmer and Russell 1986) to simulate the relative growth rates of the AC and DC components of the IHC response using a logarithmic compressive function (Zhang et al. 2001). Although increasing the degree of nonlinearity in the IHC module may have improved the model's ability to predict off-frequency TMCs, such a manipulation was not attempted as it would change an aspect of the model that was judiciously set to account for physiological data in laboratory animals. Moreover, it is possible that the Zilany et al. (2009) model does not capture all components of IHC nonlinearity as the model does not simulate the multiple mechanical drives known to influence IHC function (Guinan 2012).

The steepness of the off-frequency TMCs in some subjects may be due to individual differences in the rate of recovery from forward masking. Perhaps allowing the time constants of the temporal integrator to vary, rather than using the mean data from Oxenham (2001), would improve the model predictions in these subjects. Although mechanisms of forward masking remain a matter of debate (Oxenham 2001; Ewert et al. 2007), one potential mechanism influencing the recovery of forward masking is the MOC reflex (Jennings et al. 2009). For example, Backus and Guinan (2006) reported that cochlear gain begins to recover ~20 ms after the offset of a relatively long acoustic elicitor. As gain recovers, the amplification applied to the probe increases with probe delay, resulting in a corresponding shift in masker level at threshold and a steeper masking curve. In its current form, the model did not simulate the MOC reflex, which may explain why predictions for some subjects resulted in a shallower off-frequency TMC than for measured thresholds. The relatively steeper off-frequency TMCs in the low threshold group are consistent with a fully functional MOC reflex. In contrast, this reflex may be partially dysfunctional in listeners with hearing impairment due to OHC damage (Collet et al. 1992) and result in a relatively shallower off-frequency TMC. Previous studies have simulated the MOC reflex using the Zilany et al. (2009) model by reducing the gain of the model's OHC path (Jennings et al. 2011; Chintanpalli et al. 2012; Jennings and Strickland 2012). While these studies have effectively simulated gross changes in gain, they have not included the time course of gain reduction, which is essential for predicting TMCs. A version of the Zilany et al. (2009)

model was recently developed to include the time course of the MOC reflex (Smalt et al. 2014). This model and other models (e.g., Aguilar et al. 2013) could be used in future studies to test the hypothesis that the MOC reflex contributes to relatively steep off-frequency TMC slopes in some listeners.

Sensitivity to p_{OHC}

As the model was adjusted to simulate primarily IHC dysfunction ($p_{\text{OHC}}=0$), predicted thresholds for the off-frequency TMC increased at short delays, and the slope of the on-frequency TMC steepened at the longest probe delays (relative to simulations with purely OHC dysfunction, $p_{\text{OHC}}=1.0$). These results are consistent with greater cochlear amplifier gain and compression operating over a wider range of input levels.

As discussed by Plack et al. (2004), a hearing loss resulting from purely IHC dysfunction should result in elevated thresholds in on- and off-frequency TMCs due to an inefficient transduction process. Purely OHC dysfunction should have minimal effects on off-frequency thresholds and a larger effect on on-frequency thresholds. Nine subjects from the mid (S27, S31) and high (S43, S44, S45, S46, S47, S49, S51) threshold groups had off-frequency thresholds at the 0-ms interval that were two standard deviations above the average threshold for the low threshold group, suggesting IHC dysfunction. Of these nine subjects, only two were predicted to have more than 50% IHC dysfunction (i.e., $p_{\text{OHC}} < 0.5$; S27, S47). This failure to predict suspected IHC dysfunction may be related to relatively low f_m values in many hearing-impaired subjects (Table 2). Simulations predicted the high off-frequency TMC thresholds in subjects with suspected IHC dysfunction by decreasing f_m , rather than decreasing p_{OHC} . Thus, f_m and p_{OHC} may not be independent predictors, making it difficult to accurately estimate the degree of IHC dysfunction. A similar argument applies to k , as decreasing k will also increase predicted TMC thresholds. Although the simulations may only coarsely predict the contribution of OHC and IHC damage, they do provide evidence that adjusting OHC and IHC dysfunction is important to predicting individual differences in TMCs measured in hearing-impaired listeners.

Model Performance in On- and Off-Frequency TMCs

To further assess model performance, on- and off-frequency TMCs for a given subject were fit independently rather than together. This resulted in separate best-fitting predictors (not shown) and rms error

estimates for on- and off-frequency TMCs. The rms error of on-frequency TMC predictions was generally higher than off-frequency TMC predictions for subjects in the low threshold group (Fig. 9, upper panel), whereas no such difference was seen for the mid and high threshold groups (Fig. 9, lower panels). This suggests that future improvements to the simulations should focus on the on-frequency data. The relatively higher rms error of the on-frequency simulations may be due to the assumption that listeners with the same θ and p_{OHC} will have the same cochlear I/O function. Since θ was zero for most subjects in the low threshold group, their predictions were derived from the same cochlear I/O function. Despite this, the actual cochlear I/O functions may have differed among subjects, and this difference could partially account for the remaining individual differences in the on-frequency TMCs.

CONCLUSIONS

Model simulations suggest that individual differences in TMCs measured in subjects with a wide range of probe thresholds may be related to threshold elevation, detection efficiency, and the proportion of OHC dysfunction. These individual differences result in a wide range of compression estimates among subjects with similar audiometric thresholds, which may be due to narrow sampling of the cochlear I/O function in inefficient listeners. The increased individual differences among listeners with hearing loss in many perceptual tasks may be related to the compounding effects of degraded detection cues and detection inefficiency. Detection efficiency was correlated with temporal integration and the input SMR for the off-frequency masker, suggesting that listeners can be identified by these metrics to account for efficiency-related variance. Detection efficiency was not correlated with age after accounting for the influence of elevated thresholds. Individual differences in the steepness of off-frequency TMCs were not predicted by assuming nonlinearity of the off-frequency reference, where this nonlinearity was simulated at the basilar membrane and IHC levels. Instead the individual differences in these slopes may be related to differences in the decay of masking or the strength of the MOC reflex. Findings from this study suggest that TMCs, and perhaps other forward-masking measurements of cochlear function (e.g., growth of forward masking, psychophysical tuning curves), are subject to substantial individual differences and that these differences may be related to several factors, among which detection efficiency is preeminent in normal-hearing subjects, while threshold elevation and

the contribution of OHC and IHC dysfunction is preeminent in hearing-impaired subjects. These individual differences and their sources should be considered when using forward masking as a technique to study cochlear function. Further research is needed to identify methods for accounting for or reducing individual differences in order to infer cochlear function from behavioral data.

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APPENDIX

The best-fitting predictors were not unique in effectively predicting the TMCs of a given subject. In other words, there were other predictor combinations that produced similar rms error as the best-fitting combination. Figure 10 displays contour plots of the rms error from predictions of two representative normal-hearing (Fig. 10A) and hearing-impaired (Fig. 10B) subjects. Each contour plot shows how the rms error varies across changes in the two most sensitive predictors (f_m and k for normal-hearing listeners; θ and p_{OHC} for hearing-impaired listeners). For illustration, the remaining predictors were set at the best-fitting predictor values for a given subject (i.e., the values shown in Tables 1 and 2). Regions of low rms error in normal-hearing simulations were often confined to a restricted range of k . This range was quite narrow in subjects who were estimated to have low k (Fig. 10, S19), while subjects with high k showed a broader range (Fig. 10, S11). This suggests that the model's sensitivity to k is greater in subjects with low k , compared to subjects with high k . In contrast to k , regions of low rms error were broad for f_m and often spanned the entire f_m axis (columns of blue shading in Fig. 10A). In hearing-impaired simulations, predictions were best for several combinations of θ and p_{OHC} lying on a diagonal path from relatively low θ and p_{OHC} to relatively high θ and p_{OHC} . This suggests that if both θ and p_{OHC} were slightly increased or decreased relative to the best-fitting predictors, TMCs would continue to be well

FIG. 10. rms contour plots from simulations of two representative normal-hearing (A) and two representative hearing-impaired (B) subjects. Each point of the plot represents the rms error between the measured and predicted temporal masking curves and are shown for all combinations of the most sensitive predictors of a given subject group (k and f_m for normal-hearing listeners; p_{OHC} and θ for hearing-impaired listeners). Other predictors were held constant at the values presented in Tables 1 and 2. Lines display regions of the rms value given by the associated numbers. Cool and warm colors represent low and high rms error, respectively.

fit by the model. This interaction between θ and p_{OHC} on rms error is due to these predictors having the same general effect when adjusted individually. When holding other predictors constant, TMC thresholds increase as θ increases and as p_{OHC} decreases (i.e., more IHC dysfunction); thus, if a given θ predicts too much or too little hearing loss, p_{OHC} can be adjusted to improve the rms error.

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