

Psychophysical and modeling approaches towards determining the cochlear phase response based on interaural time differences^{a)}

Hisaaki Tabuchi and Bernhard Laback^{b)}

Acoustics Research Institute, Austrian Academy of Sciences, Wohllebengasse 12-14, 1040 Vienna, Austria

(Received 15 September 2016; revised 5 May 2017; accepted 10 May 2017; published online 12 June 2017)

The cochlear phase response is often estimated by measuring masking of a tonal target by harmonic complexes with various phase curvatures. Maskers yielding most modulated internal envelope representations after passing the cochlear filter are thought to produce minimum masking, with fast-acting cochlear compression as the main contributor to that effect. Thus, in hearing-impaired (HI) listeners, reduced cochlear compression hampers estimation of the phase response using the masking method. This study proposes an alternative approach, based on the effect of the envelope modulation strength on the sensitivity to interaural time differences (ITDs). To evaluate the general approach, ITD thresholds were measured in seven normal-hearing listeners using 300-ms Schroeder-phase harmonic complexes with nine different phase curvatures. ITD thresholds tended to be lowest for phase curvatures roughly similar to those previously shown to produce minimum masking. However, an unexpected ITD threshold peak was consistently observed for a particular negative phase curvature. An auditory-nerve based ITD model predicted the general pattern of ITD thresholds except for the threshold peak, as well as published envelope ITD data. Model predictions simulating outer hair cell loss support the feasibility of the ITD-based approach to estimate the phase response in HI listeners. © 2017 Acoustical Society of America.
<http://dx.doi.org/10.1121/1.4984031>

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Pages: 4314–4331

I. INTRODUCTION

The phase response of a transmission system such as the cochlea determines the relative timing at which different input frequencies are transmitted. Considering a natural sound consisting of multiple frequency components processed by an auditory filter (AF) with a certain characteristic frequency (CF), the temporal output pattern of the AF depends on the phase relations of the sound's spectral components in relation to the AF's phase response. This is particularly the case for higher CFs where multiple spectral components pass the AF. Therefore, the AF phase response, or more generally, the cochlear phase response, is important for encoding temporal cues such as periodicity pitch and interaural time differences (ITDs). The present study proposes and evaluates a method to determine the cochlear phase response that is based on the perception of ITD in multi-tone stimuli. Compared to existing methods, the new approach does not rely on cochlear compression and is, thus, potentially better suited to determine the phase response in listeners with cochlear hearing loss.

An established method to measure the cochlear phase response determines the amount of masking by so-called Schroeder-phase harmonic complexes (SPHCs) with various

phase curvatures on a pure tone target (Smith *et al.*, 1986). Importantly, varying the phase curvature of SPHCs does not affect their long-term power spectrum, allowing to independently study the effect of their phase curvature which results in different forms of envelope modulation (as shown in Fig. 1). For a given phase response of the AF centered on the SPHC, variable phase curvatures of the SPHC elicit different amounts of peakedness in their “internal” temporal representations (e.g., after auditory filtering). The rationale of the masking method (e.g., Kohlrausch and Sander, 1995) is that the SPHC causes a minimal amount of masking if its internal representation is maximally peaked, which is the case if its phase curvature corresponds to the inverse of the AF's phase response. Thus, assuming a uniform phase curvature of the AF, the uniform phase curvature of an SPHC that yields minimum masked threshold serves as a measure of the AF's phase response.

There are several indications that fast-acting compressive amplification by the outer hair cells (OHCs) in the cochlea is important for the masker-phase effect to occur (e.g., Carlyon and Datta, 1997; Oxenham and Dau, 2004; Wojtczak and Oxenham, 2009; Tabuchi *et al.*, 2016). The basic idea is that maskers eliciting a more peaked internal representation produce a smaller internal excitation level following fast-acting compression, resulting in less masking compared to maskers eliciting a flat representation. Perhaps the strongest indication for the importance of compression is the finding of a large masker-phase effect in forward masking, where alternative explanations for a simultaneous masking configuration, such as detecting the target in the temporal dips of a modulated

^{a)}Portions of this work were presented at the 169th Meeting of the Acoustical Society of America, Pittsburgh, PA, USA, 2015, and the 39th MidWinter Meeting of the Association for Research in Otolaryngology, San Diego, CA, USA, 2016.

^{b)}Electronic mail: Bernhard.Laback@oeaw.ac.at

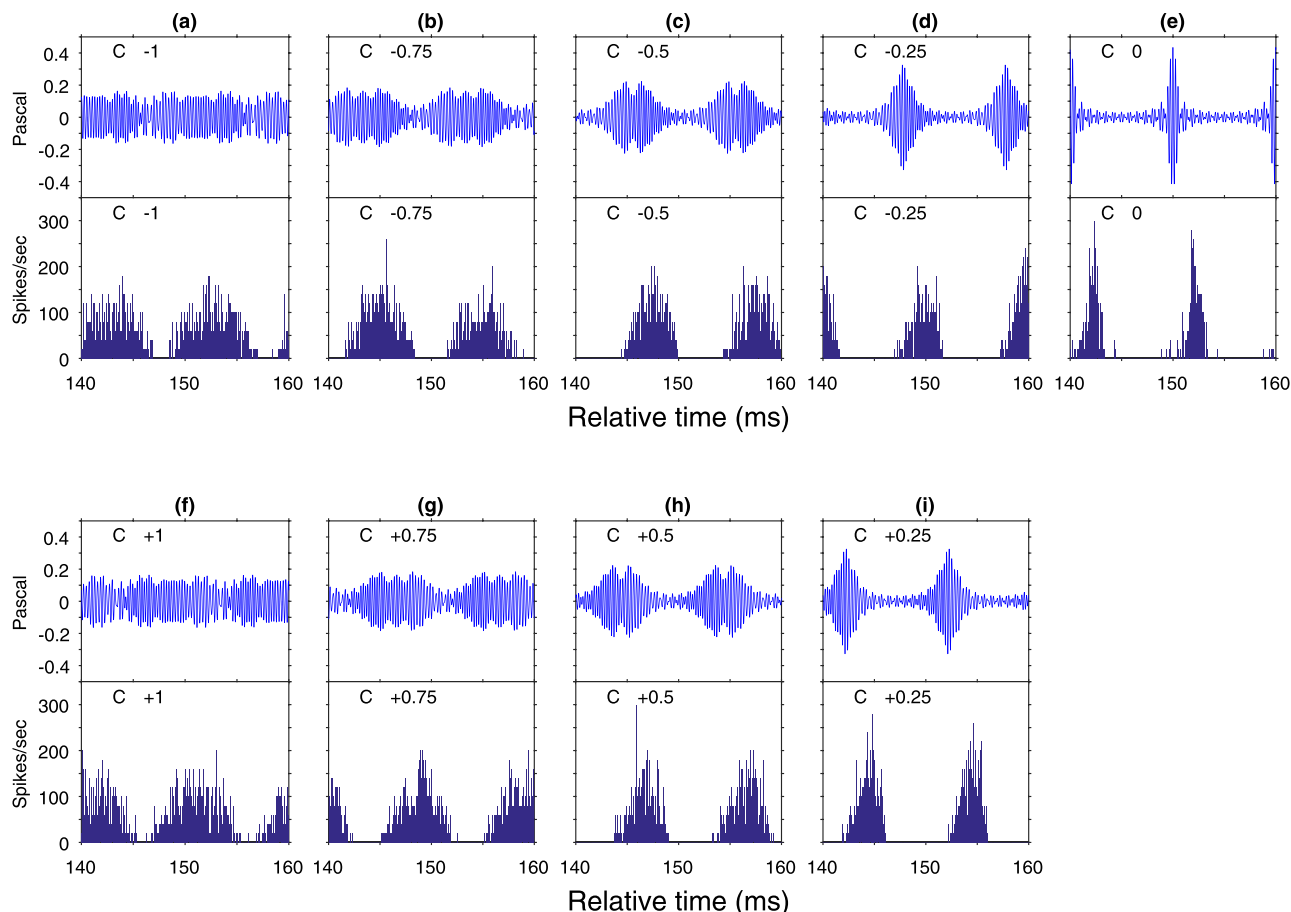


FIG. 1. (Color online) Two-period excerpts of stimulus waveforms and corresponding PSTHs of the AN front-end model (Zilany *et al.*, 2014). (a) $C = -1$, (b) $C = -0.75$, (c) $C = -0.5$, (d) $C = -0.25$, (e) $C = 0$, (f) $C = +1$, (g) $C = +0.75$, (h) $C = +0.5$, (i) $C = +0.25$. The long-term power spectra of the waveforms are constant across C 's.

masker, are not straightforward (Carlyon and Datta, 1997). Second, a recent study showed a reduction of the simultaneous masker-phase effect when adding a precursor signal supposed to reduce cochlear compression by means of activation of the efferent system (Tabuchi *et al.*, 2016). Third, listeners with cochlear hearing loss, characterized by reduced or absent OHC compression, have been shown to elicit very little or no masker-phase effect (Summers and Leek, 1998; Summers, 2000, 2001; Oxenham and Dau, 2004).

In this study, we propose an alternative approach to determine the cochlear phase response that does not rely on cochlear compression, and is, thus, potentially applicable in hearing-impaired (HI) listeners. The method exploits the listener's sensitivity to ITD of SPHC targets measured with various phase curvatures, and assumes that the peakedness of the internal target representation directly impacts ITD sensitivity. Analogous to the masking method, the SPHC phase curvature associated with the lowest ITD threshold is considered as a measure of the cochlear phase response. The method's assumption of a dependence of ITD sensitivity on the peakedness of the signal's internal envelope shape is based on several recent studies in the field of binaural hearing.

The basis for these binaural studies is the general finding that listeners are sensitive to ITD in the ongoing envelope of sounds (Henning, 1974; Yost, 1976; Bernstein and Trahiotis, 1994)

whose carrier frequencies are beyond the so-called fine-structure perception limit of about 1300 Hz (Zwislocki and Feldman, 1956). Bernstein and Trahiotis (2009), Klein-Hennig *et al.* (2011), Laback *et al.* (2011), Francart *et al.* (2012), and Dietz *et al.* (2015) went on to show that envelope ITD thresholds systematically decrease with increasing peakedness in the ongoing envelope shape, as studied by independent variation of the modulation depth or more detailed parameters of the ongoing envelope such as the flank slope and the pause time within the modulation cycle.

In all of the cited studies on envelope ITD perception, the stimulus envelopes were controlled by temporally shaping a high-frequency pure tone carrier, a process confounded to some degree with spectral alteration. In the present study, we controlled the stimuli by varying their phase properties, thus, ruling out any potentially confounding changes in the long-term power spectrum. Varying the phase curvature of SPHCs causes variable degrees of envelope peakedness, as shown in Fig. 1. In view of existing masking data at the CF region considered in our study, we hypothesized a V-shaped pattern of ITD thresholds, with lowest thresholds for slightly positive phase curvatures conveying maximally peaked internal envelopes, and elevated thresholds for more positive or negative phase curvatures conveying flatter internal envelopes. Thus, according to our assumptions, the general pattern of ITD thresholds as a function of phase curvature

should be similar to the pattern of masked thresholds obtained for similar stimuli, with the minimum representing in both cases a measure of the inverted phase response of the corresponding AF.

An important question is to what extent recently developed computational models are able to predict the effects of varying the stimulus phase curvature on ITD thresholds. Importantly, to correctly predict such data, the model requires a realistic representation of the auditory periphery, including the cochlear phase response. Figure 1 shows excerpts from the stationary part of SPHC signals used in the present study and the corresponding peri-stimulus time histograms (PSTHs) calculated by a well-established auditory-nerve (AN) model (Zilany *et al.*, 2014). The PSTHs for the different phase conditions generally resemble the temporal shape of the signal envelopes, which implies that the AN front-end model has some sensitivity to the modulation strength of stimuli. Envelope ITD thresholds for several envelope manipulations have been shown to be predictable using a simplified representation of the auditory periphery at the two ears, consisting of a linear Gammatone filter bank, square-law rectification, power-law compression, and envelope low-pass filtering, followed by an interaural comparison based on the normalized cross-correlation (NCC) metric (referred here to as NCC model, e.g., Bernstein and Trahiotis, 2009; Klein-Hennig *et al.*, 2011). However, some effects of envelope variations on ITD perception, such as temporally inverting stimuli with temporally asymmetric envelopes (e.g., steep-raising and shallow-decaying flanks) or varying the pause duration, were not fully predicted by that model (see Klein-Hennig *et al.*, 2011, and Sec. IV C 4 of the present paper). Furthermore, the Gammatone filter bank has been shown to not appropriately account for monaural phase effects (Kohlrausch and Sander, 1995; Oxenham and Dau, 2001). We therefore devised a model combining an established nonlinear model of the auditory periphery, potentially exhibiting a more realistic phase response (Zilany *et al.*, 2014), with a probabilistic interaural comparison stage. To evaluate the model's general capability in predicting envelope ITD thresholds, it was also tested on literature data on systematic variation of envelope shape parameters.

In this study we performed an experiment with seven normal-hearing (NH) listeners on the effect of systematically varying the stimulus phase curvature on ITD thresholds (Sec. II) and a follow-up experiment with two of those listeners using a finer sampling of phase curvatures (Sec. III). We then evaluated the ability of our model to predict our experimental data and relevant data from the literature (Sec. IV). Finally, we also used the model to predict how OHC loss may affect phase effects (Sec. IV C 6).

II. EXPERIMENT 1: ITD THRESHOLDS AS A FUNCTION OF PHASE CURVATURE

A. Listeners and equipment

Seven subjects aged between 19 and 33 years participated in the experiment and received monetary compensation for their participation. All had absolute thresholds of 20 dB hearing level or lower at octave frequencies between

0.25 and 8 kHz. Three of the listeners had experience from previous experiments on ITD perception. None of the authors participated in the experiment. All experiments met the ethical principles of the Acoustical Society of America.

The stimuli were generated on a computer and output via a sound interface (E-Mu 0404, Creative Professional) at a sampling rate of 96 kHz and a resolution of 24 bits. The analog signal was sent through a headphone amplifier (G93, Lake People) to circumaural headphones (HDA 200, Sennheiser). The stimuli were calibrated using an artificial ear (4153, Brüel & Kjær) and a sound level meter (2260, Brüel & Kjær). The experiment was performed in a double-walled sound booth.

B. Stimuli

The SPHCs (Schroeder, 1970; Lentz and Leek, 2001) were defined as

$$s(t) = \sum_{n=N_1}^{N_2} \cos \left[2\pi n f_0 t + \frac{C\pi n(n+1)}{N_2 - N_1 + 1} \right], \quad (1)$$

where C determines the constant phase curvature, f_0 the fundamental frequency, and N_1 and N_2 the indices of lowest and highest harmonics, respectively. The complex had a fundamental frequency of 100 Hz and the harmonics ranged from 3400 to 4600 Hz ($N_1 = 34$, $N_2 = 46$). This stimulus bandwidth is restricted compared to most published masking studies using SPHCs. One reason was to avoid the potentially confounding influence of off-frequency components half an octave or more below CF having zero phase curvature (e.g., Shera, 2001; Oxenham and Ewert, 2005; Tabuchi *et al.*, 2016). A different AF curvature within the off- and on-frequency region would violate the assumption of uniform phase curvature, as imposed by the constant curvature of the stimuli, and likely result in less pronounced phase effects. A second reason was to reduce the possibility that listeners use multiple AFs, including those remote from the target center frequency, to extract and combine ITD cues. A third reason was that all harmonics should be sufficiently above the fine-structure sensitivity limit of human listeners to avoid the contribution of fine-structure ITD cues (e.g., Zwislöck and Feldman, 1956; Brughera *et al.*, 2013), and thus potentially dominate ITD sensitivity. The stimuli had a total duration of 300 ms including 125-ms cosine-squared on- and off ramps to minimize onset and offset ITD cues. They were presented at an overall sound pressure level (SPL) of 70 dB (re 20 μ Pa). Nine C 's ranging from -1 to 1 in intervals of 0.25 were tested. Figure 1 shows example waveforms of the stimuli for C 's from -1 to $+1$. Although the long-term power spectra (across envelope periods) are constant across C 's (see Kohlrausch and Sander, 1995), the stimuli clearly differ in the peakedness of their envelopes, being largest for $C = 0$ and decreasing towards $C = \pm 1$. The ITD cue was applied to the target stimulus by delaying the entire waveform at one ear.

Interaurally uncorrelated background noise was continuously presented at 55 dB SPL to mask low-frequency cochlear distortion products. The background noises on the two ears were generated by low-pass filtering Gaussian white

noises with a second-order Butterworth filter at a cut-off frequency of 1300-Hz and with an attenuation of 12 dB/oct.

C. Procedure

Percent-correct scores in a left/right discrimination task were measured as a function of ITDs (50, 100, 200, 400, 800, and 1600 μ s). The first interval in a trial always contained the reference stimulus with *zero* ITD and the second interval contained the target stimulus with a *non-zero* ITD. The listeners indicated if the target stimulus was to the left or right of the reference stimulus using a response pad. The target ITD had equal *a priori* probability of leading at the left and right ear. Each stimulus interval was signaled visually on a computer screen, and the between-interval gap was 300 ms. Feedback on the correctness of the response was provided visually after each trial.

A block consisted of 540 presentations of nine *C*'s and six ITDs, with ten repetitions of these conditions in randomized order. Each listener completed six blocks. Thus, each combination of *C* and ITD was tested 60 times. The total testing time of the experiment amounted to about six hours per listener. We checked the ITD thresholds of each listener across blocks, but observed no systematic learning effects.

Based on the psychometric functions for each *C* and listener, ITD thresholds at the 80%-point of the psychometric function were estimated using the maximum-likelihood method in combination with a two-parameter Weibull function fit (Myung, 2003). The grand mean thresholds were calculated as the geometric means and standard deviations of ITD thresholds across individual listeners.

Before commencing the main experiment, the listeners completed a training session using the same procedure as in the main experiment. The stimulus was a bandpass-filtered

white noise spectrally centered at 4600 Hz and with a bandwidth of 1500 Hz. Blocks of 100 trials with a fixed ITD value (100, 200, 400, or 600 μ s) were run. The training started with the 600- μ s ITD and continued towards smaller ITDs until the performance for all the ITD values became better than 80% correct.

D. Results and discussion

The psychometric functions were found to monotonically increase across ITDs and the Weibull function yielded reasonable fits to each of the psychometric functions. The amount of variance explained by the Weibull fit was quantified for each *C* and listener as a percentage, with the average across all the *C*'s and listeners amounting to 89.1% (standard deviation: 10.2%). Figure 2 shows the ITD thresholds as a function of *C* for the individual listeners and the across-listener means (error bars showing ± 1 standard deviation). In some listeners, it appears difficult to determine a minimum threshold; for example, the thresholds of *C* = 0 and 0.5 in NH39, and *C* = -0.75, -0.25, and 0 in NH47, are close to each other. Despite differences across individual listeners, the across-listener means reveal a pattern of low thresholds around *C* = 0 and increasing thresholds towards *C* = ± 1 , with the exception of an elevation at *C* = -0.5 (see below). The overall pattern of ITD thresholds is consistent with previous studies in showing that the ITD sensitivity changes with the peakedness of the envelope shape (e.g., Bernstein and Trahiotis, 2009; Klein-Hennig *et al.*, 2011; Laback *et al.*, 2011). We are not aware of published data on the effects of direct manipulation of the stimulus phase properties on ITD sensitivity with which the current data could be compared. A one-way repeated-measures analysis of variance indicated a significant effect of phase curvature *C*

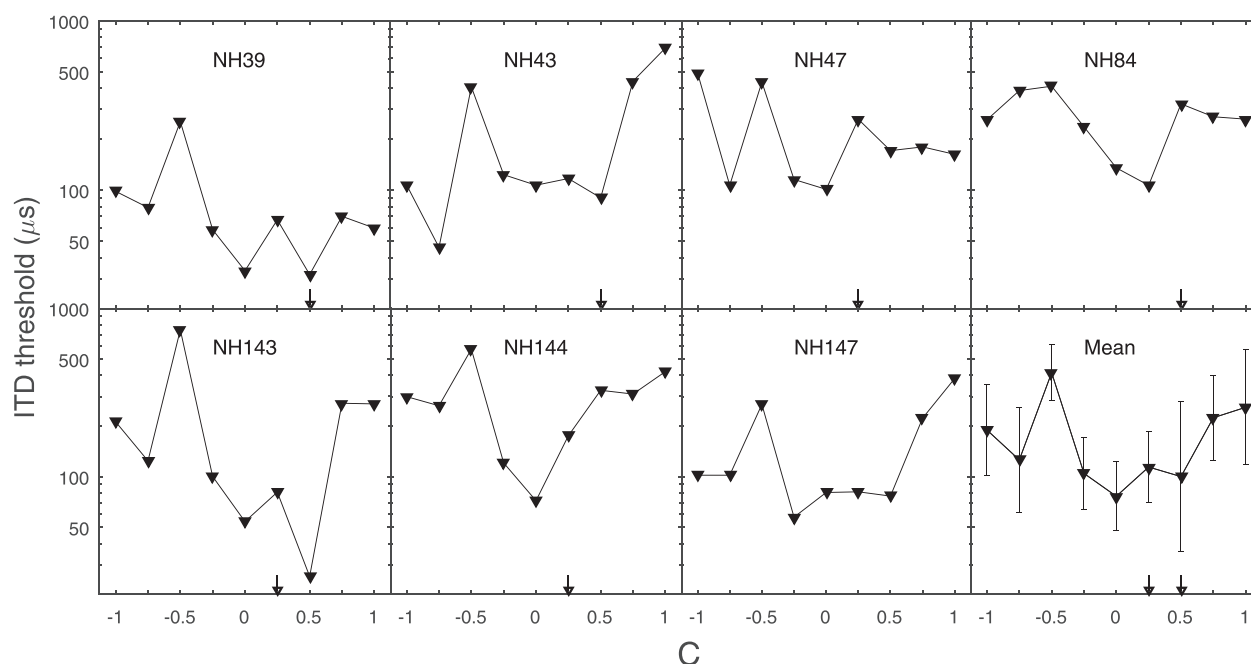


FIG. 2. Results of experiment 1: ITD thresholds are plotted as a function of *C* for individual listeners. Mean ITD thresholds across listeners (± 1 standard deviation) are shown in the bottom right panel. The small arrows indicate the *C*'s exhibiting minimum masked thresholds in a masking experiment using similar stimulus conditions with the respective listeners (Tabuchi *et al.*, 2016).

[$F(8, 48) = 7.25$, $p < 0.001$]. *Post hoc* pairwise comparisons using the Tukey LSD test indicated that thresholds do not differ significantly between -0.75 , -0.25 , 0 , 0.25 , and 0.5 ($p > 0.07$), but thresholds differ significantly between $C = 0$ versus $C = -1$, -0.5 , 0.75 , and 1 ($p < 0.03$). The phase curvatures showing the lowest mean ITD threshold (around $C = 0$) are roughly consistent with those that produced minimum masking in a study using similar stimuli in six of the listeners of the present study (between $C = 0.25$ and $C = 0.5$; Tabuchi *et al.*, 2016). For comparison, the C 's showing minimum masked thresholds for those listeners are indicated by small arrows in Fig. 2. The threshold minima are clearly more variable and less pronounced for the ITD paradigm than for the masking paradigm (see Tabuchi *et al.*, 2016). This suggests that the ITD thresholds are less stable and reliable than the masked thresholds, an issue that is addressed in experiment 2.

An unexpected non-monotonic threshold elevation (peak) was consistently observed at $C = -0.5$ for all listeners. The *post hoc* comparisons indicated that this threshold peak significantly differed from the thresholds at surrounding C 's (-0.25 and -0.75) and even from $C = -1$ ($p < 0.019$). Inspection of the stimulus envelope shapes for the stimuli with various C 's (Fig. 1) did not reveal any convincing explanation for the threshold peak in terms of envelope peakedness. In particular, the stimulus with $C = -0.5$ is not less peaked than the stimuli with C 's of -0.75 and -1 , as would be expected by its higher threshold. Because the "internal" stimulus representation actually depends on the interaction between the stimulus phase and the phase response of the cochlea, we will address this issue in more detail in the modeling section below (Sec. IV).

III. EXPERIMENT 2: ITD THRESHOLDS AT FINER STEPS OF NEGATIVE PHASE CURVATURES

This experiment served to sample the thresholds at finer steps of C in the vicinity of the threshold peak at $C = -0.5$ found in experiment 1 and check the reproducibility of the threshold peak. Two listeners (NH143 and NH144) participated in experiment 2, almost 1 year after they completed experiment 1. The equipment, stimuli, and procedure were all the same as those described in Sec. II, except that the stimuli consisted of several additional C 's and that positive C 's were not tested. The following C 's were tested: -1 , -0.75 , -0.67 , -0.59 , -0.5 , -0.42 , -0.34 , -0.25 , and 0 .

The thresholds of experiment 2 were estimated from psychometric functions by using a Markov chain Monte Carlo technique for Bayesian inference (Fründ *et al.*, 2011), which allowed us to estimate 95% confidence intervals of threshold using a bootstrap technique.¹ We observed that the Markov chain Monte Carlo technique and the maximum likelihood method (Myung, 2003) used in experiment 1 resulted in very similar threshold estimates.

A. Results and discussion

Figure 3(a) and 3(b) show the individual listener's thresholds as compared to the corresponding individual's thresholds from experiment 1 (the latter replicated from Fig. 2). The

error bars show 95% confidence intervals of the threshold estimates. For listener NH143, the thresholds for phase curvatures measured both in experiment 1 and 2 show high reproducibility, including the threshold peak at $C = -0.5$, as can be seen from the large overlap of the 95% confidence intervals. That listener's data from experiment 2 for phase curvatures not tested in experiment 1 show an additional sharp peak at $C = -0.34$. The data of listener NH144 generally show much more pronounced differences across the two experiments, although the overall pattern, including the peak at $C = -0.5$, is preserved. That second listener's data show no additional threshold peak. In summary, these data suggest some uncertainty in the ITD-threshold estimates, at least for individual listeners. Regarding the non-monotonicities in the threshold functions, the origin is unclear at this point. Modeling analyses are provided in Secs. IV C 2 and IV C 3 to explore possible explanations.

IV. MODEL

A. Rationale and general properties

In order to obtain more insight into the mechanisms underlying the experimental results, we performed a modeling approach. As a model of the auditory periphery up to the level of the AN, we used the well-established cat AN fiber model as described in Zilany *et al.* (2014) with parameters adjusted for humans. This represents the latest version (5.2) of a family of phenomenological models of the transformation of acoustic stimuli into AN discharges, including outer- and middle-ear filtering, cochlear processing, inner hair conductance as well as AN transmission properties. It has been shown to account for many effects of peripheral processing, including level dependent shifts in best frequency, suppression, and AN adaptation. Even more important for the present purpose, the model appears to provide a quite realistic auditory representation of temporal signal aspects, e.g., temporal modulation coding (Zilany *et al.*, 2009) and the phase transfer function (Carney, 1993; Zhang *et al.*, 2001; Tan and Carney, 2003; Zilany and Bruce, 2006). An attractive feature of the AN front-end is its capability of optionally simulating the effects of OHC loss associated with cochlear hearing impairment (see Zilany and Bruce, 2006). The OHC gain is controlled by changing the output of the control path (Bruce *et al.*, 2003). The simulation of complete OHC loss in the model has been shown to be associated with gain reduction in the order of 30 dB or more (resulting in increased absolute thresholds), reduced compression of the input-output function, and reduced frequency selectivity at corresponding CFs (Heinz *et al.*, 2001; Bruce *et al.*, 2003).

Varying the OHC gain allowed us to use the model to predict ITD thresholds across C in simulated cochlear hearing impairment associated with OHC loss. Note the implicit assumption of this approach that cochlear hearing loss has no consequences on auditory processing beyond the AN. Moreover, a recent animal study suggests that noise-induced hearing loss induces the selective loss of AN fibers with low and medium spontaneous firing rates (SRs, Furman *et al.*, 2013). Providing modeling results with different SRs appears

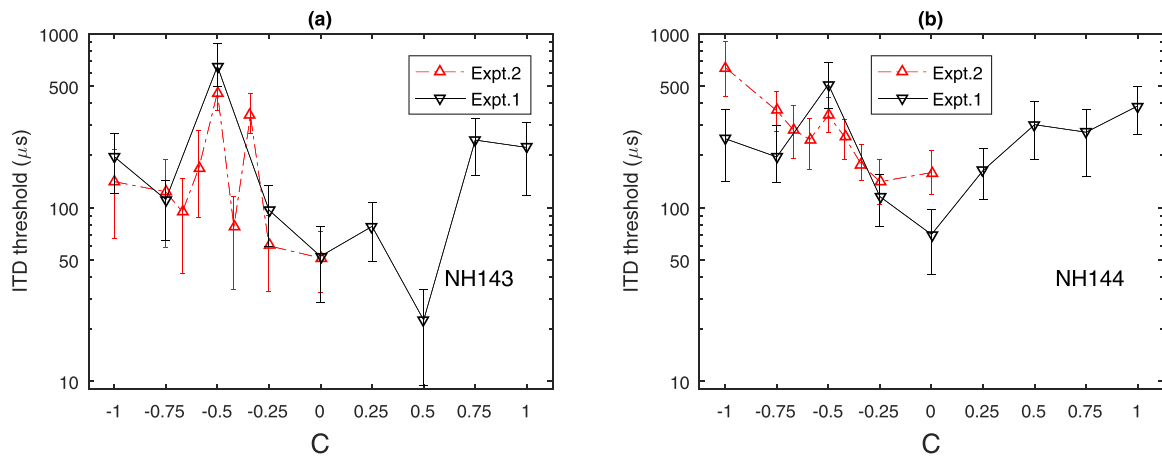


FIG. 3. (Color online) Results of experiment 2: ITD thresholds for finer C steps (upward-pointing triangles) measured in individual listeners. (a) NH143; (b) NH144. The thresholds for these listeners from experiment 1 are denoted by the downward-pointing triangles. The error bars denote 95% confidence intervals of the threshold estimates (see text).

therefore useful for understanding the behavioral consequence of OHC loss for specific fiber types.

In order to predict behavioral ITD thresholds, we combined two versions of the monaural AN front-end model with a binaural comparison stage. One well-established model of envelope-ITD perception is the NCC model. Although the NCC model has been shown to predict a variety of envelope ITD data (e.g., [Bernstein and Trahiotis, 2009](#)), [Klein-Hennig et al. \(2011\)](#) showed that the effects of some envelope manipulations cannot be predicted by that model; for example, temporally inverting an amplitude modulated signal with steep raising flanks but flat decaying flanks in each cycle results in an elevation of ITD thresholds, whereas the NCC model predicts constant thresholds. Adding adaptation loops in the NCC model, intended to replicate some aspects of neural adaptation ([Dau et al., 1996](#)), showed somewhat improved threshold predictions for some conditions, but systematic discrepancies from experimental thresholds remained ([Klein-Hennig et al., 2011](#)). The front-end of the current model appears to have the potential to even more accurately represent peripheral temporal coding properties.

For the binaural stage, we decided for a statistically motivated receiver-operating characteristic (ROC) based approach, mainly because the detailed properties of binaural cue extraction, from early stages such as the medial and lateral superior olives up to the inferior colliculus and the auditory cortex, are still matter of debate and far from being fully understood (e.g., [Grothe et al., 2010](#)). Our approach has no *a priori* assumptions on the binaural processing characteristics and can be considered as a behavioral, optimum-observer-like approach that is based on the monaural AN outputs. It thus differs from more sophisticated physiology-based binaural processing stages (e.g., [Wang et al., 2014](#); [Gai et al., 2014](#); [Dietz et al., 2016](#)).

Our model simulations were based on the left- and right-ear PSTHs of the AN model response to a stimulus, including additional 20% of the stimulus duration to account for response delay and decay. Each PSTH was based on 1000 spike train realizations. All monaural simulations were run ten times. The binaural simulations were run ten times in case

of normal OHCs and 60 times in case of OHC loss. A larger number of repetitions was chosen for OHC loss because we observed larger variance in the response as compared to normal OHCs. The reported monaural and binaural predictions are based on averaging across those repetitions. We verified for a subset of conditions that the predictions for normal OHC were the same when running either 10 or 60 repetitions, apart from the error bars becoming smaller. The model parameters of interest were the SR of AN fibers (low, medium, or high) and the OHC scaling factor (either 1 = normal or 0 = fully lost). Unless otherwise stated, the following model parameters were fixed: CF: 4 kHz; model sampling rate: 100 kHz; inner hair cell (IHC) scaling factor: 1 (normal); species: human, using basilar membrane tuning from [Shera et al. \(2002\)](#); fractional Gaussian noise type: variable; power-law implementation: approximate; bin width of the PSTH: 50 μ s. The input stimuli used in our modeling approach were the same as those used in experiment 1.

In the following subsection we describe the properties of the AN front-end model in monaurally processing our experimental stimuli. Then, we describe the binaural comparison stage and report on the ability of the complete (binaural) model to predict experimental ITD thresholds.

B. Monaural model analysis

1. Synchronization index (SI) of fundamental frequency for normal and lost OHCs

To study the temporal properties of the AN front-end model, we followed the basic idea of temporal synchronization analysis ([Goldberg and Brown, 1969](#)). To measure the synchronization of the neural response to the stimulus' temporal envelope modulation, period histograms (PHs) were first obtained by adding up the firing rates (spikes/sec) across the cycles of the PSTHs and dividing the sum by the total number of firing rates, resulting in the probability density function (the more precise term in a discrete context actually being probability mass function) as shown in Fig. 4. We then computed the SI by calculating the magnitude spectrum of the probability density function as similarly

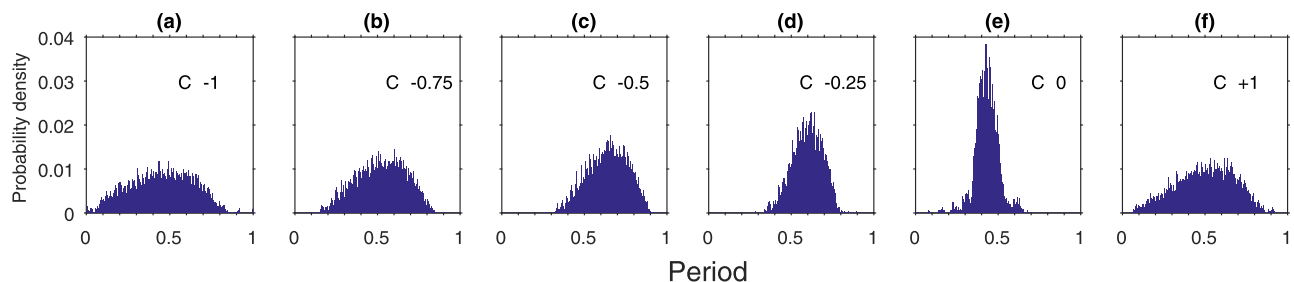


FIG. 4. (Color online) Period histograms (PH) for C 's from -1 to 0 , and $+1$ (see text). (a) $C = -1$, (b) $C = -0.75$, (c) $C = -0.5$, (d) $C = -0.25$, (e) $C = 0$, (f) $C = +1$.

done by Johnson (1980) based on the assumption that the SI is independent of the average firing rate in the analysis. The fundamental frequency (100 Hz) was the spectral component of interest for the analysis because this was the most prominent modulation frequency.

Figure 5(a) shows the SI of the fundamental frequency for normal OHCs with different SR fiber types as the parameter. The SI is largest at $C = 0$ and decreases towards $C = \pm 1$. The SI is consistent with the general pattern of ITD thresholds across C reported in experiment 1, although it does not account for the threshold peak at $C = -0.5$. We will reconsider the threshold peak in the binaural modeling. Overall, apart from the threshold peak, the SI analysis is consistent with Zilany *et al.* (2009), demonstrating that the AN model robustly predicts the effect of varying the depth of sinusoidal amplitude-modulation (AM) on physiological measures of neural envelope synchrony. It is also evident that the SIs of high-SR fibers are much lower than those of low- and medium-SR fibers. This response pattern across SR fibers is also consistent with physiological data for AM tones, which suggested that low-SR fibers are generally better phase-locked to the modulation frequency than high-SR fibers, especially for CFs below 5 kHz (Joris and Yin, 1992).

Figure 5(b) shows the SI in case of lost OHCs for the three SR fiber types. The general patterns are similar to those for normal OHCs, but there are some systematic differences. First, the SIs for the low- and medium-SR fibers are almost unchanged by OHC loss for $C = 0$, but they are lowered when C approaches ± 1 . Second, the SI for the high-SR

fibers is considerably larger in the vicinity of $C = 0$, while there is almost no difference for $C = \pm 1$. It seems that high-SR fibers with normal OHCs are saturated for the particular stimulus, whereas OHC loss shifts the dynamic range of those fibers to better encompass the dynamic range of the stimulus' temporal envelope; and therefore, results in enhanced temporal coding. This idea was confirmed by additional simulations on SPHCs with a reduced stimulus level (50 dB SPL) in normal OHCs (not shown), revealing enhanced temporal coding (in terms of the SI) for high-SR fibers. The finding is also consistent with the notion that the gain reduction associated with impaired OHC enhances neural phase locking (Kale and Heinz, 2010; Henry and Heinz, 2013). In summary, the general finding of increased difference between minimum and maximum SI in simulated OHC loss suggests that phase effects might be stronger in impaired ears compared to normal ears.

2. Firing rate for normal and lost OHCs

Figure 6(a) and 6(b) show the mean firing rate as a function of C with the three SR fibers for normal and lost OHCs, respectively. The patterns of firing rates across C are inverted compared to the patterns of SIs from Fig. 5, i.e., they show lowest rates for $C = 0$. These general patterns are consistent with the idea that instantaneous cochlear compression results in lower excitation levels and, thus, lower firing rates for more peaked stimuli (Carlyon and Datta, 1997). In this respect, they are also roughly consistent with a recent masking study using

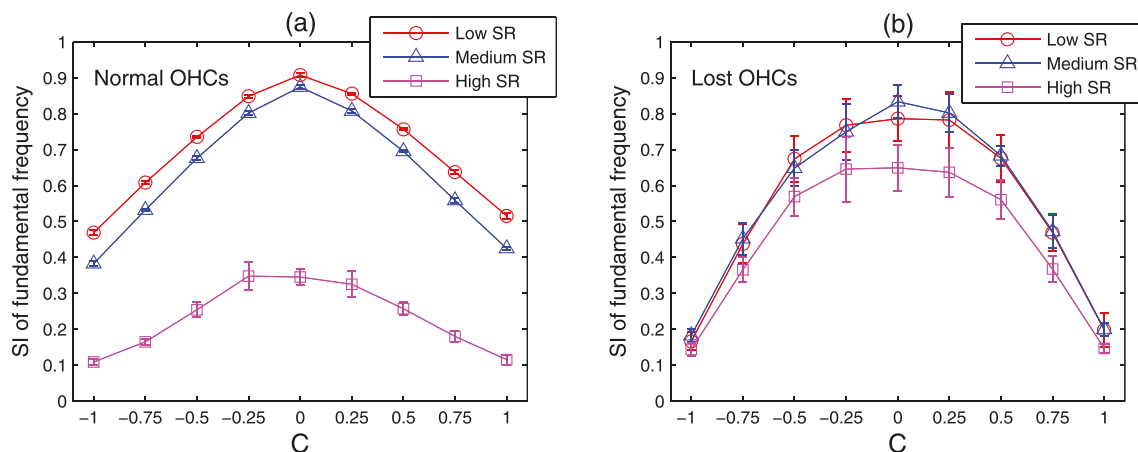


FIG. 5. (Color online) Predicted synchronization index (SI) based on the AN front-end model as a function of C . Symbols indicate the means (± 1 standard deviation) across repeated calculations for the three model fiber types with different spontaneous rates (SR). (a) Normal OHCs; (b) OHC loss.

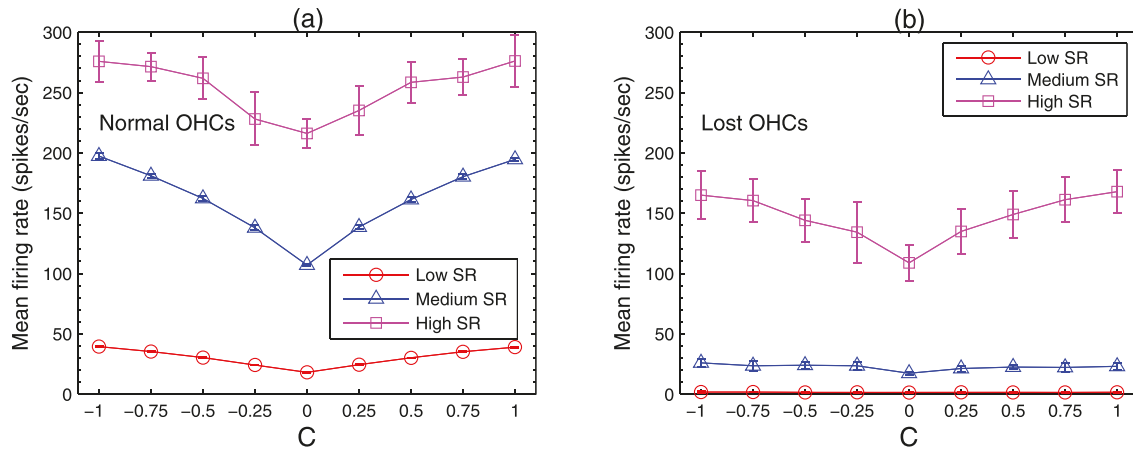


FIG. 6. (Color online) Predicted firing rate based on the AN front-end model as a function of C . Symbols indicate the means (± 1 standard deviation) across repeated calculations for the three model fiber types with different spontaneous rates (SR). (a) Normal OHCs; (b) OHC loss. Because the firing rates for low-SR fibers with OHC loss appear essentially at zero in the panel (b), the exact values (in spikes/sec) for the different C 's are denoted in the following: 1.8 ($C = -1$), 1.7 ($C = -0.75$), 1.5 ($C = -0.5$), 1.6 ($C = -0.25$), 1.4 ($C = 0$), 1.6 ($C = +0.25$), 1.5 ($C = +0.5$), 1.4 ($C = +0.75$), and 1.6 ($C = +1$).

the same stimuli as maskers (Tabuchi *et al.*, 2016), showing less masking for more peaked masker waveforms, although the minimum occurred for C 's between 0.25 and 0.5. Compared to the predictions for normal OHC function [Fig. 6(a)], the prediction for OHC loss [Fig. 6(b)] shows similar differences in the firing rates across C in case of high-SR fibers, but largely reduced differences in case of low- and medium-SR fibers. An overall reduction of firing rates as a result of OHC loss is observed, especially for the low- and medium-SR fibers, although these fibers have been shown to well encode stimulus phase differences [see Fig. 5(b)].

C. Binaural model analysis

In Sec. IV B 1, it was shown that the monaural SI analysis is consistent with the minimum ITD-threshold from experiment 1 at $C = 0$. In order to more directly predict ITD thresholds, we added a binaural processing stage which is based on minimum assumptions on the physiological mechanism. In order to predict psychophysical ITD thresholds, we compared responses of the front-end AN model to the left and right ear stimuli using the concept of ROC analysis. The left/right discrimination data underlying our ITD thresholds represent a binary classification problem which can be treated with ROC analysis. In analogy to ROC analysis used in psychophysics to describe the observer's sensitivity in a force-choice signal detection task (Green and Swets, 1974), our ROC analysis classified a given relative timing difference between the monaural AN representations, i.e., an ITD, which allowed to predict the sensitivity for that ITD. ITD thresholds were then estimated from predicted neural sensitivity estimates for different ITDs, analogous to psychophysical ITD thresholds estimated from psychometric functions. To illustrate the concept, imagine the simple case of a very short (impulsive) sound presented to a listener with a given ITD. The neural spikes in response to such a sound would be phase locked to the stimulus and, thus, the left- and right-ear PSTHs would be temporally delayed relative to each other according to the stimulus ITD. The PHs obtained from these PSTHs would likely have Gaussian-like shapes (e.g., see

Dreyer and Delgutte, 2006) and fulfill the requirements of ROC analysis to classify the ITD between them (note that a strict assumption of normality is not necessarily required for ROC analysis, as long as the underlying probability density functions decay towards both sides; e.g., see Hanley and McNeil, 1982). Because our SPHC stimuli have a periodic temporal envelope, for which, by definition, the PH is bounded by the envelope period, the question arises if the PH's shape fulfills the requirement of ROC analysis. Inspection of Fig. 4 shows that even for the most flat SPHC ($C = -1$ and $+1$), the PH decays towards both bounds of the envelope period.

The basic idea underlying our model approach is that SPHCs with different C 's result in PHs with different widths which in turn result in different ITD sensitivity. Note that our ROC analysis implicitly assumes that the process of ITD detection of our ideal observer is equivalent to the process of identifying which of the left and right ear signals is leading in time (the task the listeners actually performed in the experiments to be predicted). We assume that this simplification does not significantly affect the model's prediction power under the conditions of our study.

Our ROC model differs from the ROC analysis of binaural responses proposed by Shackleton *et al.* (2003). Their ROC analysis estimated ITD thresholds based on the neural firing rates measured from inferior colliculus neurons as a function of stimulus ITD. In contrast, our ROC analysis does not require specific properties of a binaural comparison unit because it evaluates the relative timing between monaural AN representations. Our approach is rather similar to the computations used to obtain "neurometric thresholds" in modulation detection (Johnson *et al.*, 2012; Sayles *et al.*, 2013).

1. Model details

Figure 7 depicts the structure of our complete model, combining CF-matched monaural AN pre-processing for the left and right ear channels with a binaural comparison stage: the PSTHs from the left and right ear stimuli, optionally processed by a stage of modulation transfer function (MTF; see Sec. IV C 5), are concatenated into PHs, which are then

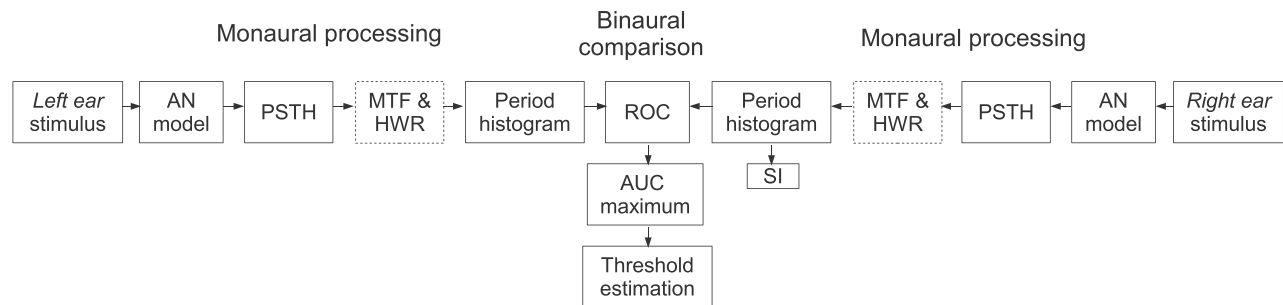


FIG. 7. Processing stages of the model used to predict ITD thresholds. The monaural processing stages for the left and right ear feed the binaural comparison stage at the center of the figure. The estimation of ITD *threshold* is based on the maximum area under the ROC curve (AUC). The stages called modulation transfer function (MTF) and half-wave rectification (HWR) were added in the “revised” model version (see Figs. 13–15). See text for details of the model.

compared by means of the ROC analysis to finally estimate ITD thresholds. Figure 8(a) shows two PHs with a relative delay (corresponding to the stimulus ITD) of $800\ \mu\text{s}$ for SPHCs with $C = -0.25$, which are referred to as leading and lagging PHs, respectively. Figure 8(e) shows example ROC curves constructed based on the cumulative probabilities of the lagging and leading PHs, from which the area under the ROC curve (AUC) is computed. For a fixed ITD ($800\ \mu\text{s}$ in this example), the binaural ROC model predicts lower AUC, i.e., lower ITD sensitivity, for flat stimulus envelopes (e.g., $C = +1$; thin solid line) compared to peaked stimulus envelopes (e.g., $C = -0.25$; thickest solid line), because the PHs for flat stimulus envelopes are flatter and therefore overlap more for a given ITD.

Before actually performing the ROC model analysis, the PHs have to be circularly shifted so that they are centered within the envelope period (10 ms for our stimuli) and thus fulfill the requirement imposed by the ROC analysis. Figure 8(a) shows the PHs already after the shifting operation. For comparison, Fig. 8(c) shows the unshifted versions of the PHs from Fig. 8(a). Note that the amount of shift required to “center” the PHs depends on the stimulus phase curvature in combination with the monaural processing delay of the auditory periphery at the given CF. Figure 8(d) demonstrates how the AUC depends on the amount of shift (within the period) for this particular example stimulus. The AUC is apparently low when the histograms are not shifted (indicated by the diamond symbol), whereas the AUC is maximal for shifts approximately between 25% and 75% of the period (the maximum indicated by the square symbol). While the shift required could be determined by some monaural criterion ensuring that the distributions are centered within the histogram window, we decided to determine it by maximizing the AUC. For each stimulus condition (i.e., each value of C), the optimal shift maximizing the AUC was determined based on the largest ITD considered ($800\ \mu\text{s}$). This optimal AUC was then applied also for all other ITDs for that condition. For simplicity, by using the term AUC in the following, we refer to the maximum (optimized) AUC. It should be kept in mind that our ROC model is intended to represent an abstract optimum-observer binaural comparison stage, which, in reality, is most likely realized by coincidence detection neurons which require no shifting operation (temporal alignment). Thus, by determining the PH shift via

maximizing the AUC, we attempt to avoid an arbitrarily unfavorable temporal alignment of the PH, which is a matter of computational modeling. Figure 8(e) shows the example condition of $C = -0.25$ and $800\text{-}\mu\text{s}$ ITD; optimizing the shift [according to the square symbol in Fig. 8(d)] gives the largest AUC (thickest solid line), whereas without the shift [according to the diamond symbol in Fig. 8(d)] the ROC curve has a “dent” that falls below the diagonal (thick dotted line). Considering only conditions including shift, decreasing the ITD from 800 to $200\ \mu\text{s}$ reduces the AUC from 0.72 to 0.56 [the latter depicted with the medium-thick solid line in Fig. 8(e)]. Finally, with zero ITD difference (thin dotted line), the ROC curve falls on the diagonal indicating chance performance (AUC 0.5).

Figure 8(b) shows the AUC as a function of ITD for example C ’s of 0 and $+1$. For visual clarity, the functions are plotted only up to $400\text{-}\mu\text{s}$ ITD. For the threshold predictions, the AUC-vs-ITD functions were obtained for each of the nine C ’s and ITDs from 0 to $800\ \mu\text{s}$ in $50\text{-}\mu\text{s}$ steps. The functions were then linearly interpolated. The arrows indicate predicted thresholds for the two C ’s at the given criterion AUC. In order to predict thresholds for the entire set of C ’s, the criterion AUC was systematically varied as the only free parameter to minimize the root-mean-square error (RMSE) between the mean experimental thresholds and corresponding predictions across all C ’s. All the RMSEs and criterion AUCs estimated in the present study are listed in Tables I and II, respectively. Throughout this paper, RMSEs were calculated in the base-10 logarithmic ITD scale and the resulting minimum RMSEs were converted back to the linear ITD scale as similarly done by Klein-Hennig *et al.* (2011). Thresholds were predicted separately for the three fiber types and two OHC scaling factors. For completeness, Table I lists also the RMSEs for the predictions that were obtained by either linearly averaging across the three SR fiber types or by weighted averaging according to the prevalence of the three fiber types in cats (Liberman, 1978). Because we observed no consistent advantage of any type of averaging, in the following we report the predictions for the individual fiber types.

2. Predicted ITD thresholds based on normal OHCs

Figure 9 shows the predicted ITD thresholds as a function of C for different SR fibers, as compared with the mean

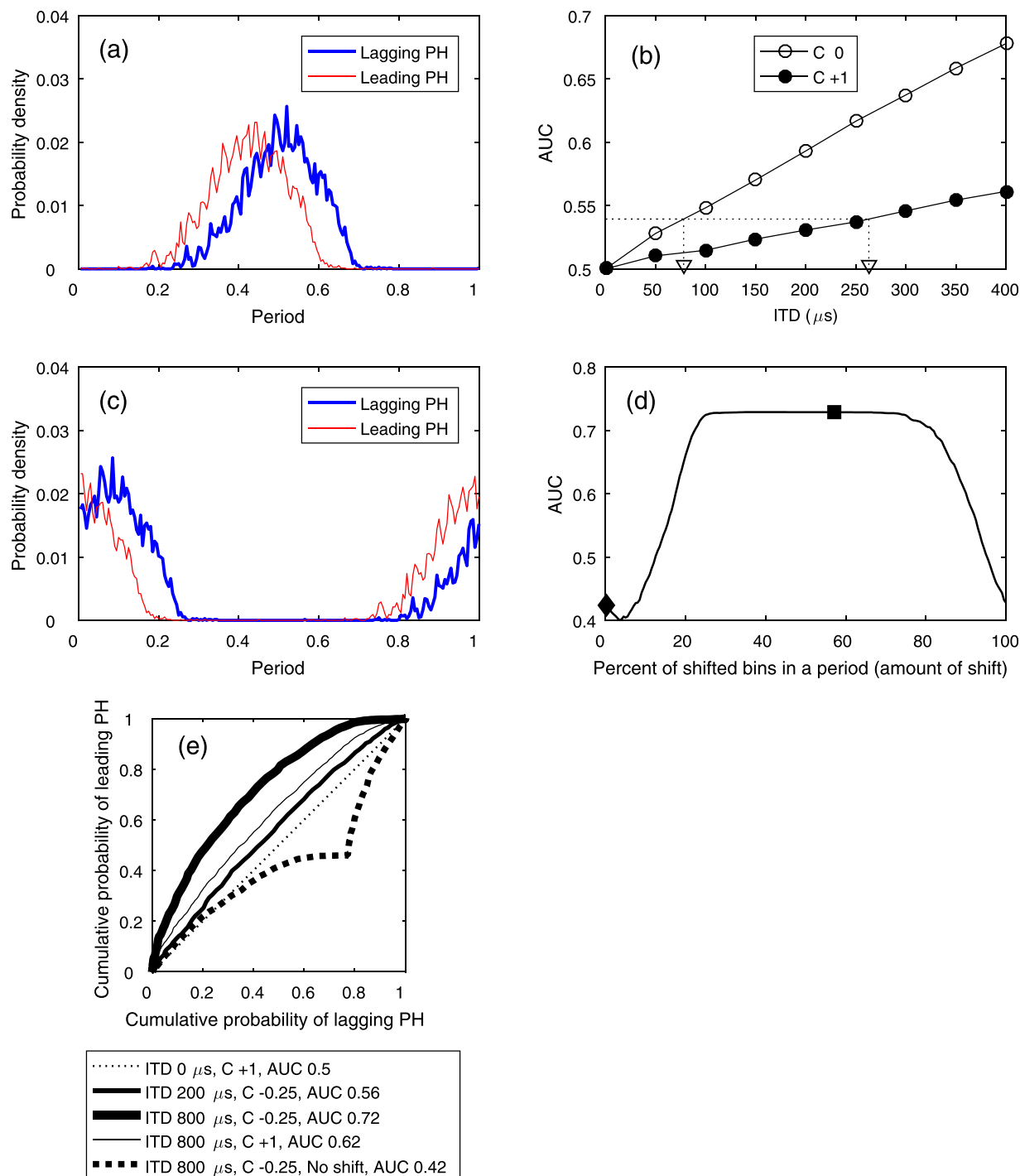


FIG. 8. (Color online) Illustration of the main steps of the binaural receiver operating characteristic (ROC) analysis. (a) Leading and lagging period histogram (PH) for $C = -0.25$, corresponding to the probability density functions of *lagging* AN responses (thick) with an ITD ($800 \mu\text{s}$ in this example) and *leading* AN responses (thin). The x axis is restricted to one period of the signal (i.e., 10 ms). The example PHs are shifted in order to maximize the area under the ROC curve (AUC). (b) AUC as a function of ITD for $C = 0$ and $+1$. The points were linearly interpolated and the inverse of the criterion AUC was defined as the predicted threshold (vertical arrows). The criterion AUC was found by minimizing the root-mean-square error (RMSE) between mean experimental thresholds and predicted thresholds. (c) The two histograms *before* applying the shifting operation, see text for details. (d) AUC as a function of the amount of shift, with the diamond showing the AUC without shift and the square showing the AUC with the optimal shift to maximize the AUC as in (a). (e) Examples of ROC curves with different ITDs and C 's with and without the optimal shift, see text.

thresholds from experiment 1. The model clearly does not account for the threshold peak at $C = -0.5$, as already suggested by our monaural model analysis. We will reconsider this point in Sec. IVC 3. Besides the threshold peak, the model well predicts the overall pattern of thresholds. Most importantly, it correctly predicts the minimum threshold at

$C = 0$ in the mean experimental data across listeners. The first and second rows of Table I indicate the RMSEs between the mean thresholds and predictions including and excluding $C = -0.5$ in the predictions, respectively. As expected, excluding the data point at $C = -0.5$ reduces the RMSEs, particularly for the low- and medium-SR fibers.

TABLE I. Root-mean-square error (RMSE) in μ s between the mean thresholds and model predictions. MTF and No-MTF refer to the binaural ROC models with and without modulation filtering and half-wave rectification, respectively. The RMSEs for the prediction averaged over the three SR fiber types are listed in the column “Mean SR,” whereas the RMSEs for the weighted average according to the prevalence of the three fiber types in cats (Low SR: 16%, Medium SR: 23%, High SR: 61%; Liberman, 1978) are listed in the column “Weighted mean SR.” The upper four rows show the RMSEs for the prediction across C ’s from the present study, whereas the lower rows show the RMSEs for attack and pause duration experiments in Klein-Hennig *et al.* (2011). The RMSEs for the normalized cross-correlation coefficient (NCC) model, the NCC model with five adaptation loops (NCC5A) and with the first adaptation loop only (NCC1A) were replicated from Table I in Klein-Hennig *et al.* (2011). The parenthesized criterion indicates that the ITD prediction of high SR fibers for the 0-ms pause duration was infinitely large due to the completely flat AUC-vs-ITD function. Minimum RMSEs are highlighted by numbers in italics.

Stimulus	ITD Model	Fig.	Low SR	Medium SR	High SR	Mean SR	Weighted mean SR	Klein-Hennig <i>et al.</i> (2011)
C	ROC, No-MTF	9	1.50	1.49	1.53	1.49	1.50	
C excluding -0.5	ROC, No-MTF		1.22	1.24	1.27	1.23	1.24	
C	ROC, MTF	14(c)	1.54	1.50	1.78	1.55	1.63	
C excluding -0.5	ROC, MTF		1.22	1.31	1.70	1.36	1.49	
Attack	ROC, No-MTF	11	1.24	1.17	1.32	1.13	1.17	
Attack	ROC, MTF	14(b)	1.12	1.29	1.35	1.24	1.29	
Attack	NCC							1.62
Attack	NCC1A							1.31
Attack	NCC5A						1.56	
Pause	ROC, No-MTF	12	1.74	1.84	(2.48)	(1.91)	(2.11)	
Pause	ROC, MTF	14(a)	1.23	1.24	1.26	1.13	1.14	
Pause	NCC							1.34
Pause	NCC1A							1.37
Pause	NCC5A							1.43

All three fiber types were found to predict the ITD thresholds about equally well. It was somewhat surprising that the high-SR fibers obviously conveyed sufficient temporal information to extract ITD cues, although the monaural SIs were found to be lower for the high-SR fibers compared to the low- and medium-SR fibers because of saturation [see Fig. 5(a)]. Note, however, that saturation of high-SR fibers is shown to play a role when adding an additional stage of modulation filtering in the model (see Sec. IV C 5 below).

We considered that one possible explanation for the threshold peak could be an effect of listeners using AFs remote from the center frequency of the stimulus in addition to or instead of the on-frequency AFs. The model was therefore rerun at CFs in $\frac{1}{3}$ octave steps from 2 to 8 kHz. The resulting predictions (not shown) revealed generally worse prediction accuracy for off-frequency CFs, with the 4-kHz CF showing the lowest RMSE. Most importantly, for none of the CFs the threshold peak at $C = -0.5$ was predicted by the model. Thus, off-frequency listening is unlikely to contribute to or explain the non-monotonic threshold peak.

TABLE II. The criterion AUCs best predicting the ITD thresholds. The AUCs for the stimuli used in the current study and Klein-Hennig *et al.* (2011) are shown in the upper four and lower four rows, respectively. See also the caption of Table I.

Stimulus	ITD Model	Fig.	Low SR	Medium SR	High SR
C	ROC, No-MTF	9	0.534	0.531	0.513
C excluding -0.5	ROC, No-MTF		0.530	0.527	0.513
C	ROC, MTF	14(c)	0.542	0.546	0.537
C excluding -0.5	ROC, MTF		0.534	0.542	0.533
Attack	ROC, No-MTF	11	0.514	0.516	0.519
Attack	ROC, MTF	14(b)	0.556	0.577	0.578
Pause	ROC, No-MTF	12	0.517	0.512	(0.521)
Pause	ROC, MTF	14(a)	0.549	0.563	0.553

3. Predicted ITD thresholds of recorded stimuli

In search of an explanation for the unexpected ITD threshold peak at $C = -0.5$, we speculated that the headphones used in our experiment might have produced some phase distortion that led to a degradation of the envelope ITD cue for that particular condition. To test this idea by means of modeling, monaural stimulus waveforms were recorded from the left and right headphones² and ITDs were subsequently imposed to generate binaural stimuli. These binaural stimuli were used as input to the binaural ROC model to predict ITD thresholds.

Figure 10 shows the predictions for low-SR fibers based on either the left or right headphone recordings (left- and right-pointing triangles, respectively). They are almost the same as those based on the original (non-recorded) stimuli (circles), without any indication of a non-monotonic peak at $C = -0.5$. The same result was found for the medium- and high-SR fibers (not shown). Moreover, we observed that the crest factors of headphone recorded waveforms are generally preserved compared to the digitally generated stimuli (not shown). Thus, the threshold peak is unlikely originating from the particular properties of the headphones.

4. Predicted ITD thresholds as a function of attack and pause duration

We tested the ROC model on literature data in order to evaluate its predictive ability in systematic manipulations of the temporal envelope shape. Klein-Hennig *et al.* (2011) systematically varied different aspects of the temporal envelope shape imposed on 4-kHz pure tones with an overall duration of 500 ms. The attack and decay flanks in each period were shaped by squared-sine functions, and the hold and pause segments had constant amplitudes at the desired level and at

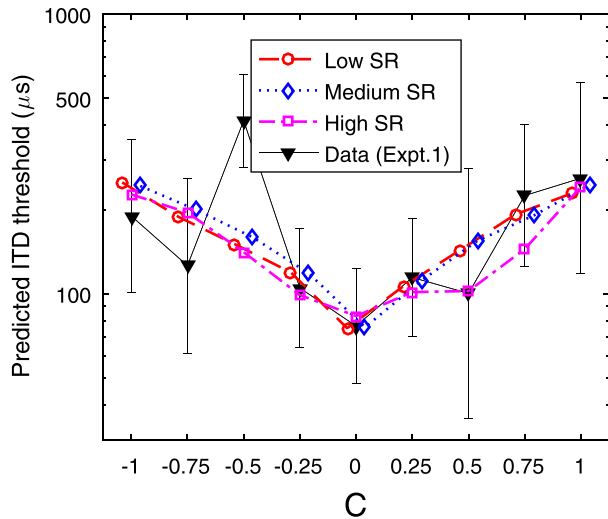


FIG. 9. (Color online) ITD threshold predictions as a function of C . The empty symbols connected by different dashed and dotted lines indicate the predictions of the initial binaural ROC model (*without* the MTF and HWR stage) for different fiber types. The filled triangles connected by the solid line denote the mean experimental thresholds replicated from Fig. 2. For clarity, some symbols are slightly shifted along the horizontal axis.

zero, respectively. We focus here on modeling the effects of independently varying the attack duration and the pause duration, as the importance of these envelope parameters was also suggested by the results of Laback *et al.* (2011). The same procedure as described in Sec. IV C 1 was used.

In their experiment on the effect of the attack duration, the hold and decay durations were kept constant, resulting in modulation rates between 35 and 50 Hz. Further stimulus details can be found in Table I of Klein-Hennig *et al.* (2011). Figure 11 shows their mean experimental thresholds across listeners and our model prediction as a function of attack duration. Both data and predictions show increasing thresholds as a function of attack duration, with our predictions falling within one standard deviation of the

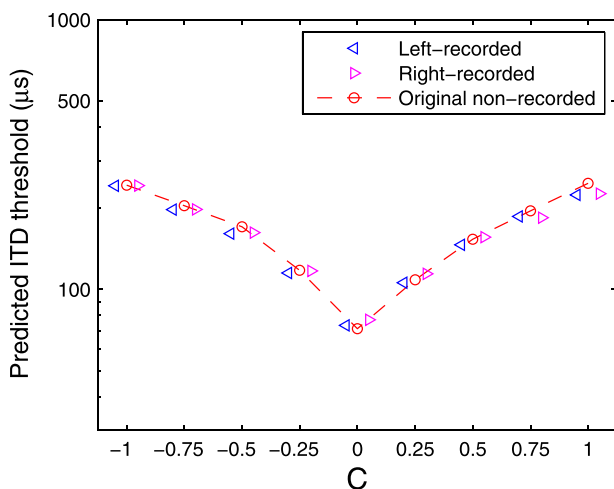


FIG. 10. (Color online) Predicted ITD thresholds from low-SR fibers as a function of C with headphone-recorded stimuli (left- and right-pointing triangles for left and right headphone outputs, respectively) and with original non-recorded stimuli (circles connected by dashed line). The predictions were made without the MTF and HWR stage. For clarity, some symbols are slightly shifted along the horizontal axis.

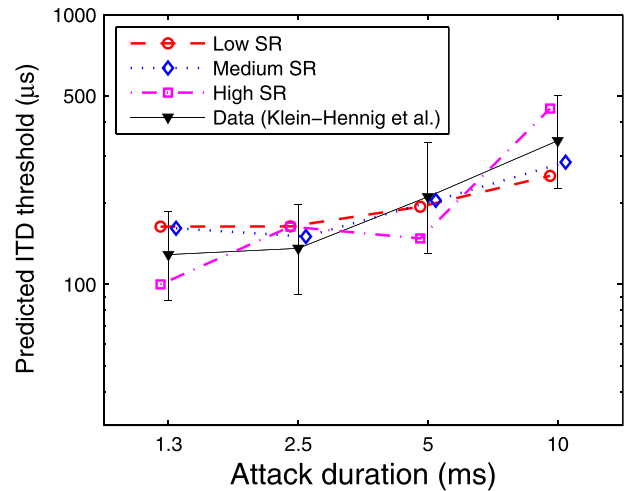


FIG. 11. (Color online) ITD thresholds and predictions for independent variation of the *attack* duration in each envelope cycle of amplitude-modulated 4-kHz tones. The filled triangles connected by the solid line denote the mean experimental thresholds (± 1 standard deviation) reported in Klein-Hennig *et al.* (2011). The empty symbols indicate predictions of the original binaural ROC model (*without* the MTF and HWR stage) for different fiber types. For clarity, some symbols are slightly shifted along the horizontal axis.

measured thresholds. In order to directly compare the performance of our binaural ROC model to the model of Klein-Hennig *et al.*, the RMSEs for their NCC model and for their NCC model with five adaptation loops (NCC5A) and one adaptation loop (NCC1A) are shown in the seventh to ninth rows of Table I. The RMSEs for our model are overall smaller compared to their models, particularly for the low- and medium-SR fibers. Overall, our model appears to well predict ITD thresholds across attack durations.

In the experiment by Klein-Hennig *et al.* on the effect of pause duration, the attack duration, decay duration, and modulation rate were all kept constant, resulting in covarying hold duration [for details see Table I of Klein-Hennig *et al.* (2011)]. Figure 12 shows the experimental thresholds together with our predictions as a function of pause duration for different fiber types.³ In line with the experimental thresholds, the predicted thresholds decrease with increasing pause duration up to 8.8 ms. For longer pause durations, however, the predicted thresholds continue to decrease up to the longest pause duration tested (17.5 ms), while the experimental thresholds are almost constant. The models tested in Klein-Hennig *et al.* (2011) showed a similar tendency. We considered that these underestimations of predicted thresholds may be due to the lack of modulation filtering in the model. This idea is further motivated and evaluated in Sec. IV C 5.

5. ITD thresholds predicted by the revised model

There are several indications from the physiological and psychophysical literature for some type of modulation filtering occurring prior to or at the level of binaural interaction (e.g., Yin and Chan, 1990; Bernstein and Trahiotis, 2002; Wang *et al.*, 2014). We supposed that such a modulation filtering may be required to obtain more similar neural

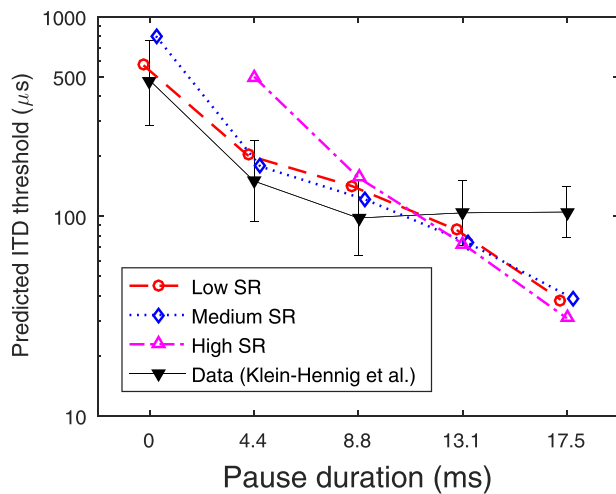


FIG. 12. (Color online) ITD thresholds and predictions for independent variation of the *pause* duration in each envelope cycle of amplitude-modulated 4-kHz tones. For other details, see caption for Fig. 11.

envelope representations for pause durations beyond about 9 ms and, thus, better prediction of ITD thresholds for these stimuli from Klein-Hennig *et al.* (2011) (see Sec. IV C 4). To that end, we added a modulation filter stage guided by the MTF measured in the medial superior olive (e.g., Yin and Chan, 1990). On the basis of Wang *et al.* (2014), we combined a first-order low-pass and a third-order high-pass filter with 300-Hz cutoff frequencies each, together forming a band-pass filter. This filter stage was applied to the PSTHs (in units of spikes/sec). To avoid negative values in the PSTH, half-wave rectification (HWR) was added subsequent to the band-pass filtering (Joris, 1996; Nelson and Carney, 2004). Note that these two new stages are performed before calculating the PH. All the model predictions presented so far were reconsidered with the revised model (see Fig. 7 for the model structure including the additional stage framed with a dotted line).

We first evaluated the revised model on the pause-duration data. Figures 13(a) to 13(d) show the PHs of low-SR fibers for the relevant long pause durations (13.1 and 17.5 ms) with and without modulation filtering (and HWR). Without modulation filtering, the PH for 17.5 ms [Fig. 13(b)] is more compact than the PH for 13.1 ms [Fig. 13(a)], which explains the lower predicted threshold for the 17.5-ms pause duration in Fig. 12. In contrast, when including modulation filtering [Fig. 13(c) and 13(d)], the PHs are much more similar and generally more narrow than those without modulation filtering. Figure 13(e) shows the AUC-vs-ITD functions corresponding to the PHs shown in Figs. 13(a) to 13(d). For clarity, the range of ITD is restricted within 150 μ s within which the predicted thresholds were anticipated. Consistent with the PHs, the narrower PHs for the model with the modulation filter result in overall larger AUC values and steeper AUC-vs-ITD functions. More importantly, the AUC-vs-ITD functions are similar for the two pause durations with modulation filtering (empty symbols), whereas they differ more without modulation filtering (filled symbols). As expected from these AUC-vs-ITD functions, the predictions of the

revised model [Fig. 14(a)] better represent the saturation of thresholds at longer pause durations as compared to the original model (Fig. 12). Across all the pause durations, the predictions fall almost within one standard deviation of the actual thresholds across listeners. The revised model also produced valid threshold predictions for high-SR fibers. The RMSEs are overall lower than those for the different model versions presented in Klein-Hennig *et al.* (see Table I).

Figure 14(b) (middle panel) shows the performance of the revised model for Klein-Hennig's data on the effect of attack duration. Compared to the original model version (Fig. 11), the predictions are comparably accurate (see also RMSEs in Table I). This suggests that the additional stage of band-pass filtering (and HWR) is not important for predicting the thresholds across attack durations.

Figure 14(c) (bottom panel) shows the predictions of the revised model for our thresholds across C obtained in experiment 1. In case of low- and medium-SR fibers, the predictions remain generally accurate, showing the minimum at $C = 0$. The predictions for high-SR fibers show a pattern completely inconsistent with the experimental data. As shown in the monaural SI calculations, high-SR fibers appear to be saturated for the particular stimulus level. While this did not sufficiently impair the temporal code in the model version without the MTF, the application of modulation filtering for the high SR fibers *increased* the relative peakedness of the PH for $C = +1$ and -1 , whereas it *decreased* the peakedness of the PH for $C = 0$ (not shown), suggesting that the modulation filtering degraded the temporal code of high SR fibers. Note that the experiments by Klein-Hennig *et al.* (2011) were performed at lower stimulus levels (between 60 and 65 dB SPL), which may explain the relatively better predictions for this fiber type. Notably, as for the original model version, none of the fiber types in the revised model accounted for the threshold peak at $C = -0.5$.

In summary, including a modulation filter allows to better account for a larger body of envelope ITD data, particularly when considering low-SR fibers. For high-SR fibers, the effect of the modulation filter on the prediction power is either beneficial (pause duration), marginal (attack duration), or largely harmful (current experiment 1). The different stimulus levels in the different experiments appears to contribute to the differential effects of the modulation filter. While the temporal code in high-SR fibers appears to be degraded compared to low- and mid-SR fibers (as shown by the monaural SIs provided in Sec. IV B 1), it appears to be just sufficient for extracting ITD cues without modulation filter (Fig. 9). In contrast, the addition of the modulation filter seems to render those ITD cues unreliable [Fig. 14(c)].

6. ITD threshold predictions with OHC loss using the revised model

In Sec. I, we hypothesized that the reduced compression associated with OHCs loss may enhance stimulus phase effects on ITD sensitivity. The monaural model analysis supported this idea by showing larger differences in SI across C 's with OHC loss compared to normal OHCs (Fig. 5). We therefore speculated that predicted ITD thresholds would

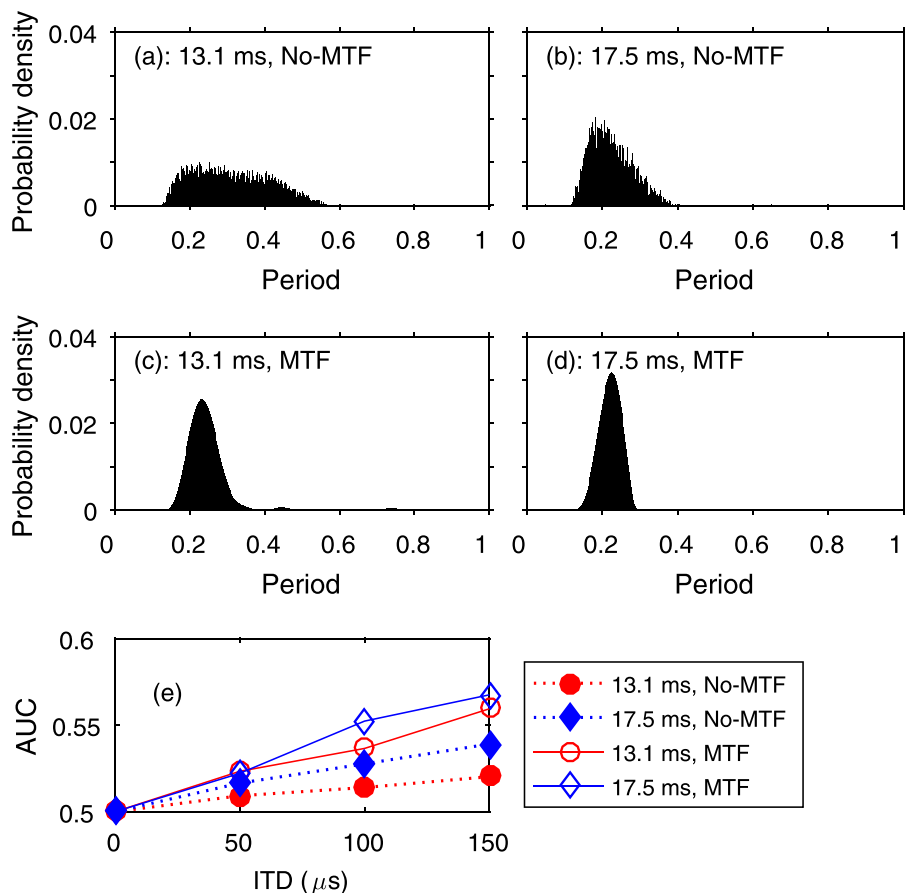


FIG. 13. (Color online) Period histograms (PHs) of low-SR fibers for stimuli with long *pause* durations, 13.1 and 17.5 ms, in each envelope cycle of amplitude-modulated 4-kHz tones as used in Klein-Hennig *et al.* (2011). (a) and (b) PHs *without* MTF and half-wave rectification (HWR). (c) and (d) PHs *with* MTF and HWR. (e) AUC as a function of ITD for the pause durations 13.1 and 17.5 ms. The empty and filled symbols denote the AUCs with and without MTF and HWR, respectively.

also differ by a greater amount across C 's with OHC loss compared to normal OHCs. Because experimental data with HI listeners were not available to optimize the AUC criterion at threshold, we used the same AUC criterion, i.e., decision criterion, for each fiber type that was found to be optimal to predict the NH listeners' data (see also Table II). This assumption is not unreasonable given that binaural processing is often assumed to be normal in listeners with cochlear hearing loss.

Figure 15 shows the resulting predictions of ITD thresholds across C with OHC loss, using the revised model. Consistent with the SI predictions, for low-SR fibers, OHC loss results in a larger range of ITD thresholds across C as compared to normal OHCs [see corresponding predictions of the revised model in Fig. 14(c)]. Medium- and high-SR fibers provide very similar patterns of predicted thresholds, with a markedly smaller range of thresholds compared to the low-SR fibers. Note that with normal OHCs the predicted threshold pattern for high-SR fibers was found to be completely inconsistent with the data. The relatively better predictability for high-SR fibers with OHC loss compared to normal OHCs supports the above-mentioned interpretation that OHC loss shifts the response level below the saturation region for the fiber's operation range at the given stimulus level. The thresholds predicted for OHC loss tend to be higher compared to those predicted for normal OHCs. This appears consistent with the overall higher SI values in normal OHCs, at least for the low- and medium-SR fibers, and with the overall higher spike rates. Thus, the predicted thresholds with OHC loss being overall larger than those with normal OHCs is

broadly consistent with experimentally measured envelope ITD thresholds for AM tones being larger in HI than in NH listeners (Lacher-Fougère and Demany, 2005). Overall, these simulations support the idea that the lack of compression in cochlear hearing loss may enhance the differences in ITD thresholds across C 's, at least in low-SR fibers.

V. GENERAL DISCUSSION AND CONCLUSIONS

The goal of this study was to evaluate the idea that ITD thresholds vary as a function of the signal's phase curvature and thus may provide a measure of the phase response at the AF centered at the stimulus. To that end, experiment 1 measured ITD thresholds using SPHCs centered at 4 kHz with various phase curvatures quantified by the parameter C . The frequencies of all spectral components were sufficiently high to ensure that they were not resolved and could not provide fine-structure ITD cues. The results showed significant and systematic effects of C on ITD thresholds across our test group of seven NH listeners. Given that only the phase properties of the harmonic complexes were manipulated, keeping the power spectrum constant, the effect can only be due to the temporal interaction of the stimulus' spectral components, resulting in envelope ITD cues. According to our hypothesis, the different amounts of envelope peakedness for the stimuli with different C 's (Fig. 1) would result in different envelope ITD thresholds. As such, the reported ITD thresholds reflect the exclusive effect of changes in the temporal envelope shape, without any confounding changes of

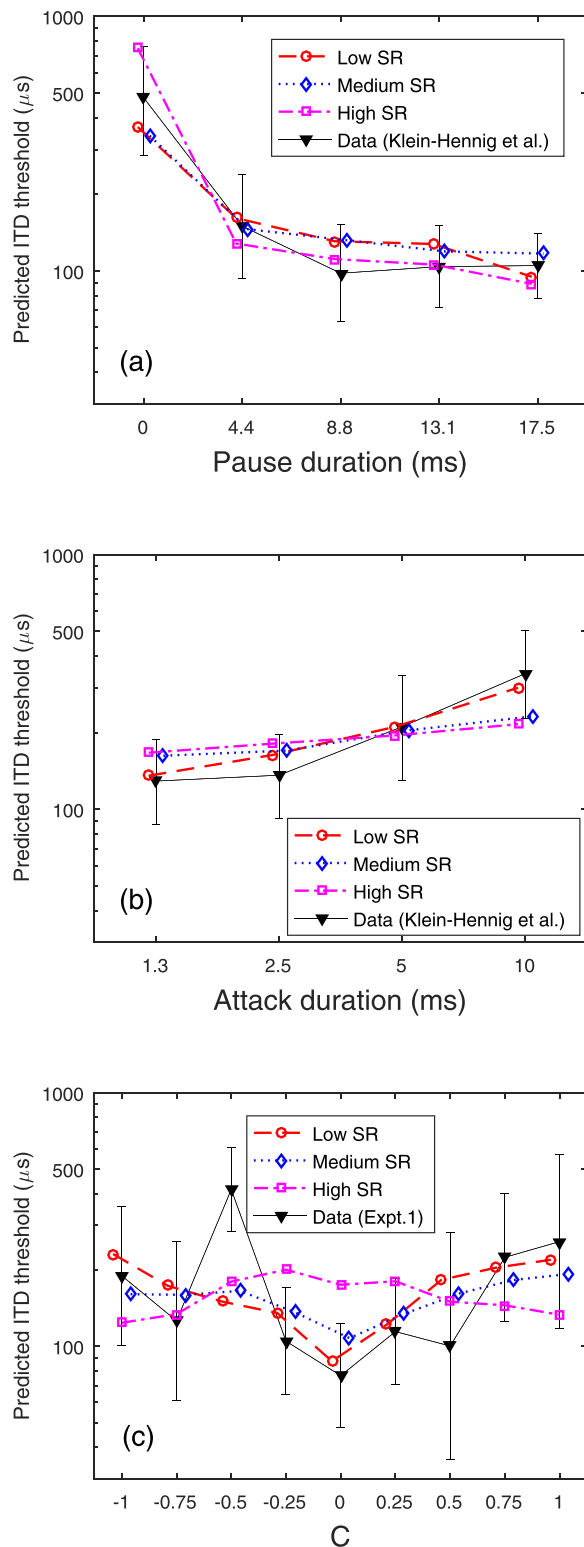


FIG. 14. (Color online) ITD threshold predictions of the “revised” binaural ROC model, which includes the MTF and HWR stage. (a) ITD thresholds as a function of *pause* duration (data from Klein-Hennig *et al.*). (b) ITD thresholds as a function of *attack* duration (data from Klein-Hennig *et al.*). (c) ITD thresholds as a function of C . For comparison, the corresponding predictions *without* the MTF and HWR stage are shown in Figs. 12 and 11, and 9, respectively.

the long-time stimulus spectrum, which has, to our knowledge, not been shown before.

Our results potentially provide insight into the phase response of the AF centered at the stimulus. It was assumed

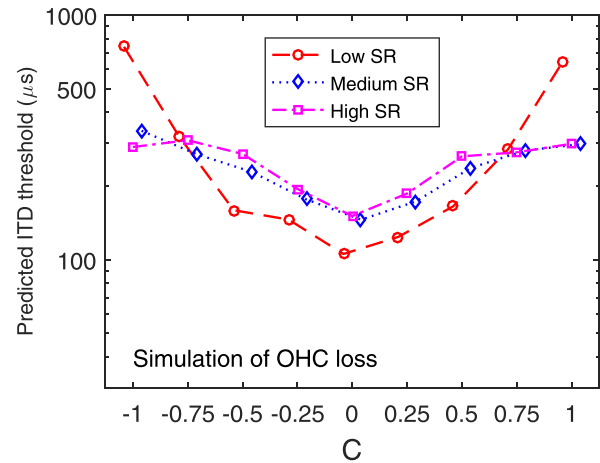


FIG. 15. (Color online) ITD threshold predictions as a function of C simulating complete OHC loss, using the “revised” binaural ROC model. The AUC criteria for the individual fiber types were taken from the corresponding simulations with normal OHCs in Fig. 14(c) (see also Table II).

that the “internal” envelope representation, i.e., after passing the AF, is important for the ITD extraction process and that ITD thresholds would be lowest for stimuli with the most peaked “internal” envelope. On average across listeners, the minimum ITD threshold was found at $C = 0$. According to the idea that the stimulus phase curvature resulting in minimum ITD threshold reflects the mirrored phase curvature of the auditory periphery, this would suggest that the phase curvature in the peripheral auditory system at the CF centered at our stimuli (4 kHz) is approximately zero. On a more detailed level, the ITD data show a relatively large amount of uncertainty about the position of the minimum along the C scale both within and across listeners, which could be somewhere between -0.25 and 0.5 . In contrast, masking data from an experiment involving similar stimuli and largely the same listeners (Tabuchi *et al.*, 2016) revealed a more robust minimum that occurred between $C = 0.25$ and 0.5 . Together, these results seem to suggest that the current ITD paradigm does not provide sufficiently stable estimates of the minimum in ITD sensitivity across C 's that could be used to infer the cochlear phase response in individual NH listeners.

An unexpected non-monotonous threshold elevation (peak) was consistently observed for a particular phase curvature, namely at $C = -0.5$. Because this peak was rather unexpected (we are not aware of any masking data using SPHC stimuli showing such a peak), we took some effort to evaluate and understand its origin. First, in a follow-up experiment with two of the listeners using a finer sampling of C 's (experiment 2), we replicated the presence of the peak, and found even a secondary peak in one listener. Second, we ruled out a potentially confounding influence of the headphones' transfer function. Third, we performed a modeling analysis⁴ to evaluate if the combination of the auditory periphery model up to the level of the AN (Zilany *et al.*, 2014) and a probabilistic interaural comparison stage can predict the pattern of experimental data. It was shown that the model predicts the overall pattern of results, i.e., an essentially V-shaped pattern, but it does not predict the peak

at $C = -0.5$. As an additional check, we inspected the temporal response to SPHCs with various C 's of a time-domain cochlear model which has been shown to well predict human otoacoustic emission data (Verhulst *et al.*, 2012). The temporal envelope peakedness of the model responses showed a very similar dependency on C as we observed for the responses of the AN model used as a front-end of our ITD model, with no indication for a non-monotonic behavior at C 's around -0.5 . In summary, assuming no errors in our experimental setup (which we checked carefully), and assuming the general appropriateness of the model (see below), all these results appear to suggest that the AF phase response at 4 kHz may have some yet undiscovered feature producing a blurry "internal" envelope for C 's around -0.5 . While the phase response of the AN front-end model has been fitted to AN data from the cat (Zilany and Bruce, 2006), it is conceivable that the human phase response differs in some aspects which affects the salience of the "internal" envelope ITD cues but not the amount of masking for certain negative stimulus phase curvatures. Note that direct and non-invasive measurement of the cochlear phase response in humans is difficult (e.g., see Paredes Gallardo *et al.*, 2016).

In order to evaluate the wider applicability of our model, we predicted published data on the effect of systematic variation of basic envelope shape parameters on envelope ITD sensitivity (Klein-Hennig *et al.*, 2011). Data on the effect of the attack duration within each modulation cycle were well predicted by the model, whereas data on the effect of the pause duration within the modulation cycle were only partly predicted. For large pause durations (>9 ms), the model systematically underestimated the measured thresholds. Considering that this discrepancy may be due to an improper envelope representation available to the interaural comparison stage of our model, we included an envelope modulation filter stage which was inspired by band-pass-like "MTF" characteristics of binaural envelope processing (Yin and Chan, 1990; Wang *et al.*, 2014) and follows also the general idea of other established auditory models of envelope filtering (e.g., Ewert and Dau, 2000). Adding this stage clearly improved the predictability of the pause-duration data and predicted the data of attack-duration and C 's as well as the model without the modulation filter. The revised model provided slightly better predictions than the well-established NCC model as well as a variant of it including a stage simulating peripheral adaptation (Klein-Hennig *et al.*, 2011). Interestingly, while the NCC model has been shown to be most successful in predicting envelope ITD data when including a 150-Hz modulation low-pass filter (e.g., Bernstein and Trahiotis, 2002), including such an envelope filter in our model actually reduced the predictability of the pause-duration data. The more physiology-based MTF stage included in our revised model has a clearly higher cutoff-frequency of the low-pass filter component (300 Hz). The properties of the modulation filter should be further evaluated and optimized based on a larger body of experimental data.

The ITD model in its current form is applicable only for periodic signals because it is based on a probabilistic

analysis of the PH. For application with non-periodic stimuli, the PH stage could be replaced, for example, by a shuffled cross-correlogram analysis (Joris, 2003). A recent ongoing study (Prokopiou *et al.*, 2015) using such an approach reported successful prediction of the effects of envelope-shape manipulations reported in Laback *et al.* (2011), similar to those tested in Klein-Hennig *et al.* (2011).

One motivation for the present study was to evaluate the general feasibility of a method to measure the AF phase response, applicable also in listeners suffering from cochlear hearing impairment characterized by OHC loss (Oxenham and Bacon, 2003). While the established masking paradigm for determining the AF phase response relies on fast-acting cochlear compression (e.g., Oxenham and Dau, 2004; Tabuchi *et al.*, 2016) which is absent or reduced in case of OHC loss, the ITD-based approach investigated in the present study does not rely on that requirement. Our model predictions showed that OHC loss actually increases the effect of the stimulus phase curvature on ITD thresholds, as compared to NH listeners. Our monaural SI analysis (Fig. 5) suggested that this can be attributed to two effects: for low- and medium-SR fibers, OHC loss decreases the SI for C 's approaching -1 or $+1$ and has no effect for C 's close to zero, together enhancing the effect across C 's. For high-SR fibers, in contrast, OHC loss enhances the SI for C 's close to zero and has no effect for C 's approaching -1 or $+1$. On the basis of these predictions, ITD thresholds may be expected to vary more across C in actual HI listeners compared to NH listeners. Thus, using an ITD-based method may be a viable approach to determine the phase response of AFs in cochlear hearing loss.

An interesting observation from our modeling using the "revised" version of the ITD model was that the temporal code provided by high-SR fibers for our medium-level (70 dB SPL) stimuli appears to be susceptible to response saturation effects, resulting in unreliable ITD threshold predictions for that fiber type. In contrast, the low- and medium-SR fibers provided much more accurate ITD threshold predictions, obviously because they were not affected by response saturation effects at the given stimulus level. Listeners may thus focus on low- and medium-SR fibers to extract ITD cues from these stimuli. It might, however, pose a problem for listeners suffering from noise-induced hearing loss where low- and mid-SR fibers may be predominantly impaired (Furman *et al.*, 2013). Future experiments with listeners having cochlear hearing loss with different origins might address these issues.

Before extending the approach of the present study to actual HI listeners in future investigations, the open issues regarding the ITD paradigm mentioned above need to be addressed. A reliable measure of the AF phase response may then make it possible to incorporate the subject-specific phase response in the signal transmission of hearing devices in order to enhance the salience of temporal cues, most importantly rate pitch and ITD. Enhanced access to pitch and ITD cues would likely improve auditory communication in challenging listening environments involving multiple sound sources.

ACKNOWLEDGMENTS

We thank two anonymous reviewers for providing helpful comments on an earlier version of the manuscript. We also thank Michael Mihocic for his assistance in writing software programs for the experiments (*ExpSuite*), Katharina Zenke for her assistance in collecting preliminary data, and Dr. Piotr Majdak and Dr. Thibaud Necciari for helpful comments. This work was supported by the Austrian Science Fund (FWF, P24183-N24).

¹MATLAB code of a Markov chain Monte Carlo technique (Fründ *et al.*, 2011) is available at <http://psignifit.sourceforge.net/>.

²For the recordings, the headphones stimuli were sent through an artificial ear (4153, Brüel & Kjær) and a sound level meter (2260, Brüel & Kjær), and digitized by a sound interface (E-Mu 0404, Creative Professional) at a sampling rate of 48 kHz. Recordings were made using the free audio software Audacity (Free Software Foundation, Boston, MA, version 2.11; <http://audacityteam.org/>).

³For the high-SR fibers, at the pause duration of 0 ms the AUC-vs-ITD function was completely flat around AUC 0.5 and thus did not allow to estimate a threshold as shown in Fig. 12.

⁴Matlab codes of the current model are available at <http://amtoolbox.sourceforge.net/>.

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