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Basilar-membrane responses to multicomponent (Schroeder-phase) signals: Understanding intensity effects

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Harmonic complexes comprised of the same spectral components in either positive-Schroeder (+Schr) or negative-Schroeder (−Schr) phase [see Schroeder, IEEE Trans. Inf. Theory **16**, 85–89 (1970)] have identical long-term spectra and similar waveform envelopes. However, localized patterns of basilar-membrane (BM) excitation can be quite different in response to these two stimuli. Measurements in chinchillas showed more modulated (peakier) BM excitation for +Schr than −Schr complexes [Recio and Rhode, J. Acoust. Soc. Am. **108**, 2281–2298 (2000)]. In the current study, laser velocimetry was used to examine BM responses at a location tuned to approximately 17 kHz in the basal turn of the guinea-pig cochlea, for +Schr and −Schr complexes with a 203-Hz fundamental frequency and including 101 equal-amplitude components from 2031 to 22 344 Hz. At 35-dB SPL, +Schr response waveforms showed greater amplitude modulation than −Schr responses. With increasing stimulation level, internal modulation decreased for both complexes. To understand the observed phenomena quantitatively, responses were *predicted* on the basis of a linearized model of the cochlea. Prediction was based on an “indirect impulse response” measured in the *same* animal. Response waveforms for Schroeder-phase signals were accurately predicted, provided that the level of the indirect impulse used in prediction closely matched the level of the Schroeder-phase stimulus. This result confirms that the underlying model, which originally was developed for noise stimuli, is valid for stimuli that produce completely different response waveforms. Moreover, it justifies explanation of cochlear filtering (i.e., differential treatment of different frequencies) in terms of a linear system. © 2003 Acoustical Society of America.

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I. INTRODUCTION

Perception and discrimination of auditory stimuli can be studied with a great variety of signals. Commonly used classes of stimuli include (this compilation is not at all exhaustive) tone signals, noise signals, impulsive signals, and multicomponent signals. A similar variety of stimuli can be applied in research into cochlear function. To facilitate understanding auditory processes, the stimulus signals used in both psychophysical and physiological studies are often “synthetic”, i.e., not recorded from natural sounds but generated for a specific purpose.

In most cases of observing responses of the auditory system to these stimuli, *nonlinear* phenomena in the auditory system play a part, and one goal of hearing research is to bring unity to the description of these effects. In this respect the methodologies of psychophysics and physiological research have generally been very different. One of the purposes of the present study is to attempt to bring these fields closer together. To this aim, very specific stimuli have been used in experiments on movements of the basilar membrane

(BM) in test animals, and the results can be used to try to understand data of psychophysical experiments in humans and birds in which the same stimuli were used—but in a different setting, namely, one involving auditory masking.

Two important properties of cochlear mechanical non-linearity are that response magnitudes show compressive growth and reduced frequency selectivity as input levels increase. This applies to all classes of stimuli listed above. Surprisingly, these nonlinear changes in magnitude can, in specific cases, have remarkably little effect on the timing properties of the response. Responses of the BM to impulse stimuli, measured at a fixed basal location *tuned to a high frequency* (e.g., 17 kHz), show almost the same zero-crossing times for various levels of stimulation. Concurrently, the trajectories of the instantaneous frequency with time (“glides”) follow the same pattern over a large (>80-dB) input range (de Boer and Nuttall, 1997, 2000; Recio *et al.*, 1998; Recio and Rhode, 2000). The upward frequency glides in the high-frequency region reflect dispersion in the traveling wave, whereby lower-frequency components of the

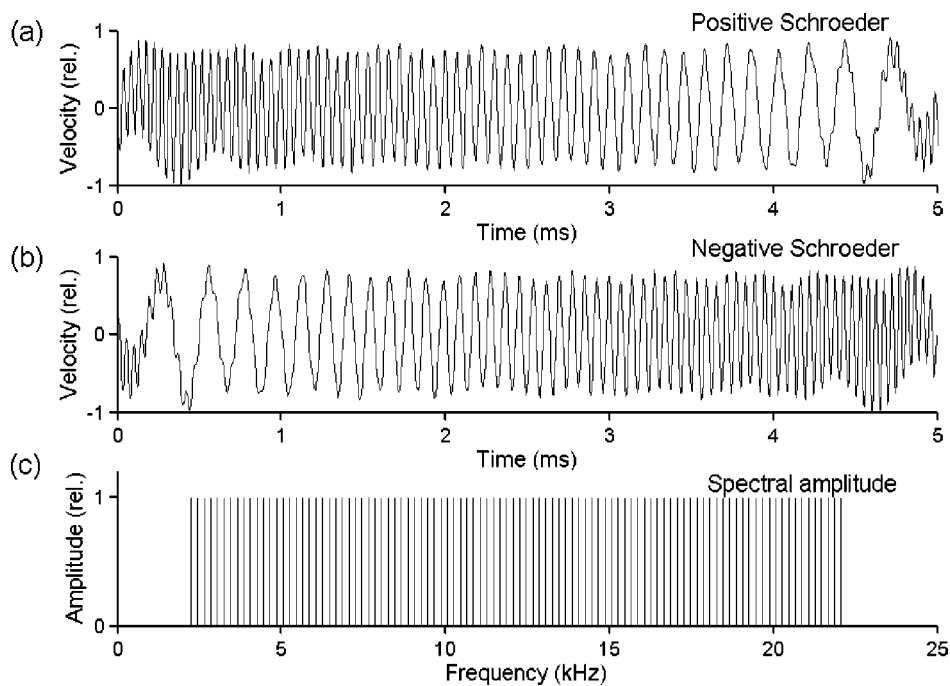


FIG. 1. Schroeder-phase signals. Panel (a): Positive Schroeder waveform, shifted over 4.5 ms with respect to origin of signal buffer. Panel (b): Negative Schroeder wave, shifted over 0.5 ms with respect to origin of signal buffer. Panel (c): Amplitude spectrum.

stimulus are traveling faster and arrive at the measurement location sooner than higher frequencies (Pickles, 1988; Shera, 2001). In different terms, the glide phenomenon is related to negative curvature of response phase with increasing frequency. Similar frequency glides are present in derived impulses responses of auditory-nerve fibers in basal regions (Møller and Nilsson, 1979; Carney *et al.*, 1999).

In many listening situations these intrinsic frequency glides in BM response are of little perceptual significance. However, psychophysical results involving “Schroeder-phase” harmonic complexes indicate an important influence of this dispersion on auditory processing (Smith *et al.*, 1986; Kohlrausch and Sander, 1995). These complex stimulus signals are periodic and contain a finite number of equal-amplitude harmonics with phases θ_n (with $n = 1, 2, 3, \dots$) based on the following formula, proposed by Schroeder (1970):

$$\theta_n = \pm \pi n(n-1)/N_c, \quad (1)$$

where θ_n is the phase in radians of the n th harmonic and N_c is the total number of harmonics. The quadratic term in Eq. (1) causes a non-negative second derivative of the phase; in the sequel we will refer to *phase curvature* as directly related to this second derivative. Waveforms of the two Schroeder-phase signals used in the present study are plotted in Fig. 1, panels (a) and (b); see Sec. II for more details. Note that the waveform amplitudes are almost constant. The legend describes how much the two waveforms are shifted with respect to the “zero point” in time. The positive-Schroeder (in what follows, designated by “+Schr”) complex is produced with Eq. (1) with the “+” sign and each period is observed to contain a high-to-low frequency glide. The negative-Schroeder (designated by “-Schr”) complex is produced with the “-” sign in Eq. (1), and it is a time-reversed version of the +Schr complex, each period containing a low-to-high frequency glide. Panel (c) of Fig. 1 shows the amplitude spectrum of the Schroeder signals. The Appendix describes a

fundamental problem in interpreting and unwrapping phase values in terms of Eq. (1) when signals—stimuli as well as responses—are given or acquired as *waveforms*. The Appendix illustrates that the second derivative is preserved in the unwrapped phase, a most important property in the context of this paper. It also contains an introduction into the nature of responses to Schroeder-type signals.

Psychophysically, +Schr stimuli are often found to be less effective maskers than -Schr complexes composed of the same harmonic components (Smith *et al.*, 1986; Kohlrausch and Sander, 1995; Carlyon and Datta, 1997a,b; Summers and Leek, 1998; Summers, 2000; Oxenham and Dau, 2001a,b). In effect, pure-tone masked thresholds may differ by more than 20-dB between +Schr and -Schr maskers with identical (long-term) magnitude spectra. The common interpretation of these masking differences is that the upward frequency glide that is inherent in the BM impulse response partially compensates for the downward glide in the +Schr complex to produce a more modulated (“peakier”) internal response pattern for +Schr than -Schr stimuli. These high-amplitude peaks in the response to the +Schr complex alternate with low-amplitude (“quiet”) periods, where the presence of an added target signal is readily detected. This results in reduced masking effectiveness for the +Schr complex. A recent physiological study has provided support for this difference in modulation of the BM response to Schroeder signals: Recio and Rhode (2000) reported more modulated (peakier) BM excitation for +Schr than -Schr complexes in chinchillas.

In the psychophysical studies the difference in masking effectiveness between +Schr versus -Schr complexes varies with level (Carlyon and Datta, 1997a,b; Summers and Leek, 1998; Summers, 2000). This may indicate that the relative peakiness of BM responses produced by +Schr and -Schr complexes may also be level dependent. A number of level-dependent changes in BM response properties may influence

the peakiness of responses to these stimuli. In effect, we know much about how stimulation level influences BM response properties. With increasing level, the low-frequency tail of the frequency response at a fixed BM location grows linearly, while responses near the *characteristic frequency* (CF) grow less than linearly (Rhode, 1971; Johnstone *et al.*, 1986; Ruggero *et al.*, 1997). As a result, a sharply-tuned bandpass response at low levels gradually turns into a broadly tuned, more or less low-pass response as level increases. In addition, the frequency producing the largest response at a fixed basal BM location (the *best frequency*, BF) shifts downward with increasing level. Both of these changes lead to an increased influence of frequencies well below CF on BM responses at high levels (relative to frequencies in the CF region). These level-dependent changes in the magnitude response could enhance or reduce peakiness in BM response envelopes depending on the relative influence of low- versus high-frequency components in controlling response modulation. In addition, although the temporal properties of BM impulse responses are nearly invariant with level, phase responses to tones and clicks do show some level dependence. For frequencies just below CF, responses to low-level stimuli show phase leads relative to higher-intensity inputs. Just above CF, the pattern is reversed and low-level inputs show phase lags relative to higher-level signals (Rhode and Robles, 1974; Geisler and Rhode, 1982; Sellick *et al.*, 1982; Nuttall and Dolan, 1996; Ruggero *et al.*, 1997; Recio *et al.*, 1998). These differences indicate level-dependent changes in the temporal responses to near-CF frequencies which could also have significant effects on BM response envelopes for a range of signals.

In the present study we examined how presentation level influences BM responses to +Schr and -Schr stimuli at a fixed BM location in guinea pigs. The observed responses were put into relation with *impulse responses* of the BM at comparable stimulus levels. The impulse response of the BM can be found in two ways.

- (i) With an acoustic impulse as stimulus (called the “direct” impulse response); and
- (ii) With a wideband flat-spectrum noise stimulus (called the “indirect” impulse response). It has been shown by de Boer (1997) that, in view of an extremely general type of *nonlinear model of the cochlea*, the “indirect” impulse response as determined by method (ii) is to be preferred for analysis. The indirect impulse response is found from the cross-correlation function of input and output signals, and it is this cross-correlation function that shows the characteristic “peakiness” that we associate with an “impulse response” (de Boer and Nuttall, 1997).

In a linear system, direct and indirect impulse responses are identical. In that case, the impulse response will allow accurate prediction of responses to other inputs such as tones and harmonic complexes. Despite nonlinearity in BM response properties, measured direct impulse responses have shown fairly good agreement with indirect impulse responses (de Boer and Nuttall, 1997). The same was found for direct impulse responses computed from BM responses to tones

(Robles *et al.*, 1976; Recio and Rhode, 2000). In addition, responses to pure tones can be predicted very well from (indirect) impulse responses (de Boer and Nuttall, 2002). It is the average amplitude of the BM response that is the prime determinant of nonlinearity (de Boer and Nuttall, 2000); hence, levels have to be matched for optimum results. As said earlier, we are studying the relation between responses to Schroeder stimuli and (indirect) impulse responses. In point of fact, we will try to predict responses from stimulus signals and impulse responses. If that prediction succeeds, we have the means to explain all our observations and to extrapolate these and other findings to psychophysics.

II. DATA ACQUISITION AND PROCESSING

A laser velocimeter was used to examine BM movements in the basal turn of the cochlea for eight pigmented guinea pigs. The preparation, measurement, and data-processing techniques were as described previously by de Boer and Nuttall (1997). Velocities were measured at a location tuned to approximately 17–17.5 kHz at low levels. The custom-designed data presentation and collection hard- and software operated at a clock frequency of 208 kHz and continuously presented a (circular) 4096-point data array while simultaneously sampling the BM response. The period of the generated stimulus as well as of the response signals was ~20 ms. Test stimuli were +Schr and -Schr complexes with a fundamental frequency of ~203.1 Hz and were the sum of 101 equal-amplitude components between 2031 and 22 344 Hz; see Fig. 1, panel (c). These 101 components were assigned phase values based on the “+” or “-” versions of Eq. (1) to produce the waveforms plotted in Fig. 1, panels (a) and (b). The complete 4096-point data array contained four periods of the waveform, each corresponding to ~5 ms. Velocity responses to pseudorandom noise stimuli and to +Schr and -Schr complexes were collected over a range of stimulus levels. Schroeder stimuli were presented at 35, 55, 75, and 95 dB SPL, and noise stimuli at levels from 10 to 100 dB SPL, in steps of 10 dB. All these levels refer to the power contained in one octave from 10 to 20 kHz.¹ Stimuli were calibrated with a $\frac{1}{4}$ -in. condenser microphone placed in an ultrasmall coupler. In earlier experiments we confirmed the calibration *in situ* with a probe microphone at the entrance of the bony auditory meatus. Analysis and processing of data were done with MATLAB[®] in conjunction with routines written in TURBO PASCAL[®].

III. RESULTS

A. “Indirect” impulse responses

Panel (a) of Fig. 2 shows waveforms of “indirect” impulse responses of the BM for one animal at levels from 40 to 100 dB SPL. The curves have been normalized to the same rms amplitude to facilitate comparison of the temporal waveforms. Responses have amplitudes that first grow and later decrease with increasing time. As stimulus level increases, the later portions of the response become smaller in comparison to earlier regions. The zero crossings indicate an oscillation frequency that increases with time (the “glide”). Note the temporal alignment of the oscillations across levels:

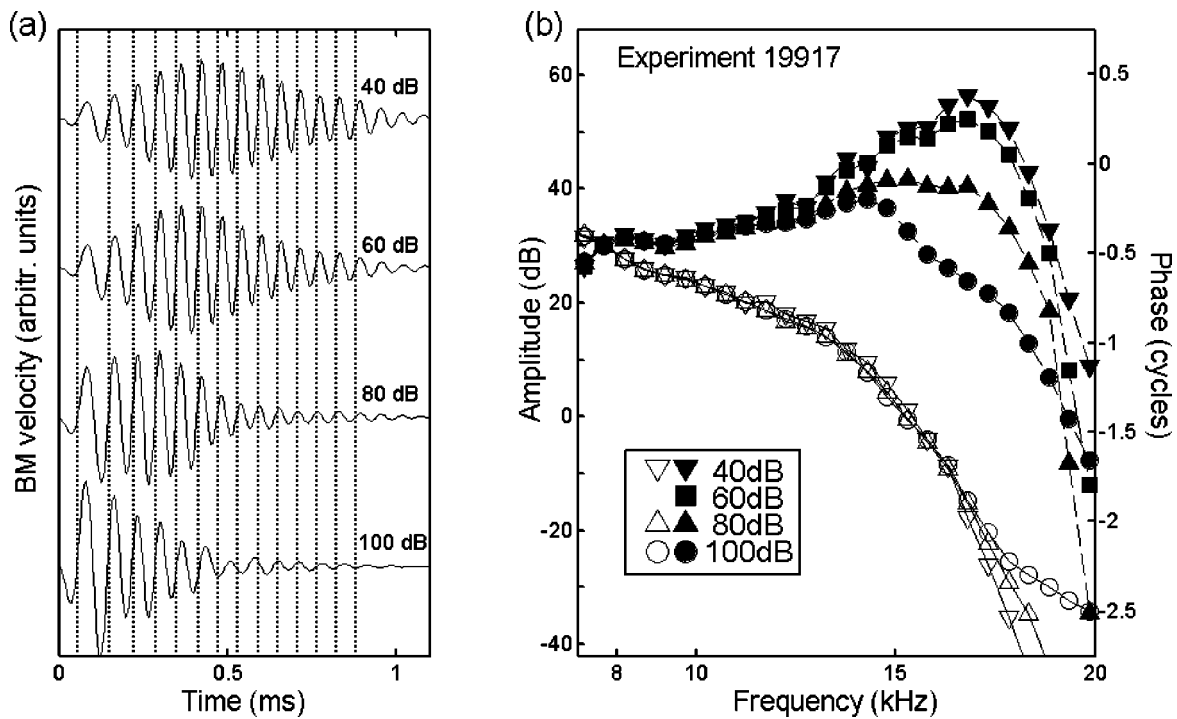


FIG. 2. Characteristics of “indirect impulse responses.” Panel (a): Waveforms for various stimulus levels, normalized *re*: rms amplitude. Measured responses are corrected for the stapes response. Input levels are in dB SPL for the 10–20 kHz octave. Curves are displaced vertically with respect to one another. Panel (b): Amplitude and phase spectra corresponding to the waveforms. Filled symbols show response amplitudes and depict “gain” since data have been normalized to the stapes velocity at the same stimulus level. Unfilled symbols indicate phase. The 60-dB phase curve was nearly identical to 40-dB data and is not included in panel (b). Note that a linear frequency scale is used in panel (b) to accurately represent the curvature in phase in the CF region.

the locations of the zero crossings are nearly invariant with level (see the vertical dotted lines). These temporal patterns are representative of all eight animals.

Panel (b) of the figure shows amplitude and phase values based on Fourier transforms of the waveforms in panel (a). Spectral amplitude values have been normalized with respect to the stapes response, *taken at the same stimulus level* so that the ordinate depicts cochlear gain. The amplitude of the frequency response shows fairly narrow tuning at low levels with a characteristic frequency (CF) of about 17 kHz. As reported in many previous studies, the amplitude curves show “tip” and “tail” regions which respond differently to level variation. The boundary between these regions is about half an octave below CF, i.e., around 12 to 13 kHz. For low frequencies, the response is linear with stimulus amplitude, and, consequently, the curves overlap. At higher levels the response for high frequencies is compressive (it varies less than linearly with stimulus amplitude). As the level increases, the amplitude in the tip region thus diminishes relative to that at lower frequencies, tuning broadens, and the amplitude peak (at the *best frequency*, or BF) moves to a lower frequency.

In contrast to the amplitude curves, the phase curves are fairly similar across stimulus levels. In detail, the phase curves also show evidence of different patterns in tip and tail regions. In the tail region (below around 13 kHz), phase change is approximately linear with frequency, signifying a constant delay. Here, the phase curves for different stimulus levels almost perfectly overlap. At higher frequencies, phase values have an increasing negative slope (i.e., negative curvature) with increasing frequency. This indicates that greater

delays are associated with high frequencies than low ones. In the CF region the phase curves show small, but systematic, level-dependent changes as detailed in the Introduction. Note that a linear frequency scale is used in panel (b) to accurately represent the curvature in phase in the CF region. Wave dispersion, which is the cause of frequency-to-place mapping in the cochlea, shows up in the form of phase curvature—on both a logarithmic and a linear frequency scale.

B. Responses to harmonic complexes

Figure 3 shows typical response waveforms, measured at a medium stimulus level (55 dB), for a +Schr and a -Schr stimulus for one animal. The abscissa covers the most interesting part of the response, over 3 ms. The legend tells how much the waveforms are shifted in time. The data are normalized to the same rms value. The 3-ms temporal interval allows inspection of the frequency glides with time. The +Schr response (upper waveform) has a high-to-low glide, in the same direction as the stimulus signal [compare Fig. 1(a)]. In contrast, the response to the -Schr stimulus (lower waveform) has a low-to-high glide [compare Fig. 1(b)].

Figure 4 shows data in a form emphasizing the *envelope*, over a range of stimulus intensities. The envelope was determined from an expansion to the *analytic signal* of all waveforms. In each panel the responses are shown normalized to the same rms value. The left-hand and middle columns show BM responses to the two harmonic complexes at stimulus levels of 35, 55, 75, and 95 dB SPL. The right-hand column shows indirect impulse responses at similar levels. In each panel of the figure, one full period (~5 ms) is shown.

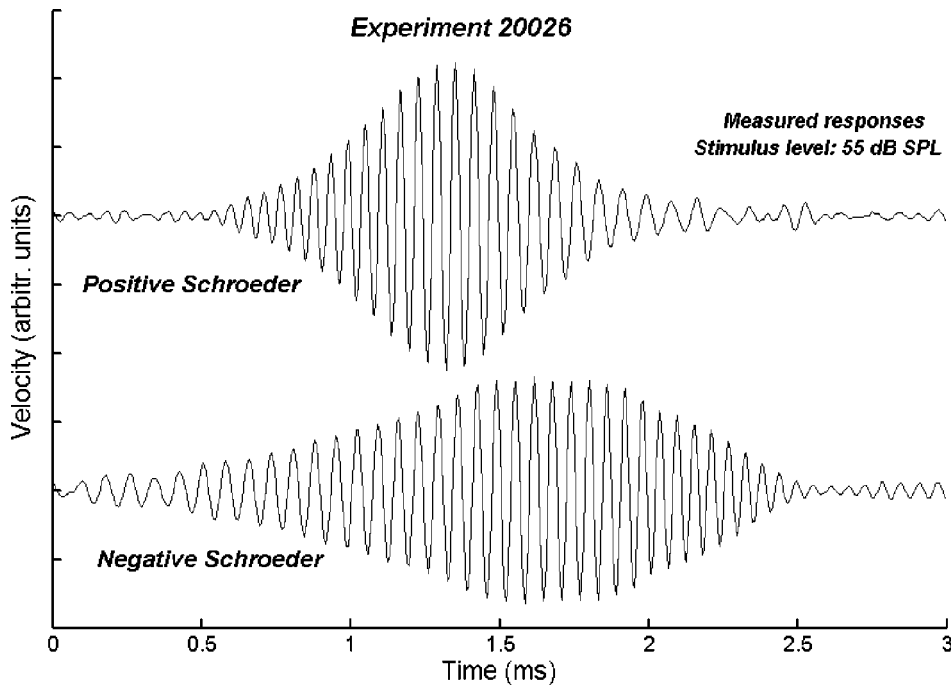


FIG. 3. Examples of response waveforms for Schroeder-phase stimuli. Stimulus level: 55 dB SPL in the octave from 10 to 20 kHz. Responses normalized to equivalent rms amplitude. Positive Schroeder response is plotted above negative Schroeder response, which has been shifted over 3 ms to the left.

Indirect impulses responses become peakier and response peaks move earlier with increasing level. These changes are consistent with a greater influence of low-frequency parts of the input on BM responses at high levels. (see the Introduction and Fig. 2). That is, given that low frequencies propagate more rapidly and less dispersively than higher frequencies, peakier and earlier impulse responses should occur with increasing level as low-frequency portions of the impulse come to dominate the internal response.

At low levels, +Schr stimuli produce peakier BM response patterns than -Schr stimuli. As level increases, both responses are showing less and less peakiness, but the -Schr response shows this effect more clearly. These results are

consistent with previously reported BM displacement data for chinchillas (Recio and Rhode, 2000). Although response envelopes for +Schr and -Schr stimuli differ (at low input levels in particular), responses are similar in overall energy. That is, rms values of responses to the two stimuli (at a constant input level) are nearly equivalent. This differs from the earlier work involving chinchillas where responses to -Schr stimuli had higher rms values (Recio and Rhode, 2000).

The stimulus- and level-dependent changes in BM response envelopes shown in Figs. 3 and 4 were present for all eight animals. Figure 5 shows results for another animal, organized in the same way as Fig. 4. As can be seen in both figures, responses to the Schroeder-phase stimuli often have

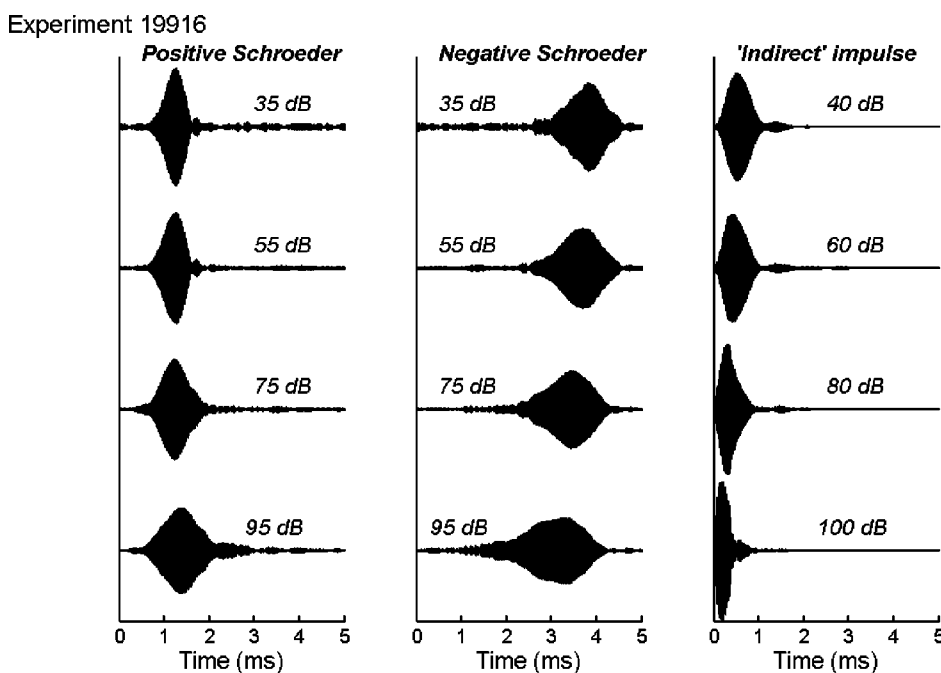


FIG. 4. Envelopes of responses to Schroeder signals and indirect impulse responses. Left panel: responses to positive Schroeder (+Schr) signals, for four different stimulus levels. Center panel: responses to negative Schroeder (-Schr) signals, for the same levels. These responses have been shifted by 4.25 ms to the left. Right panel: indirect impulse responses at four levels. Note that the responses become wider with increasing stimulus level for the two Schroeder-phase signals while the impulse response narrows. In addition, the +Schr response shows a steady increase in the latency of its peak as level increases while, for both the -Schr and the indirect impulse response, response peaks move earlier with level (see the text).

Experiment 19917

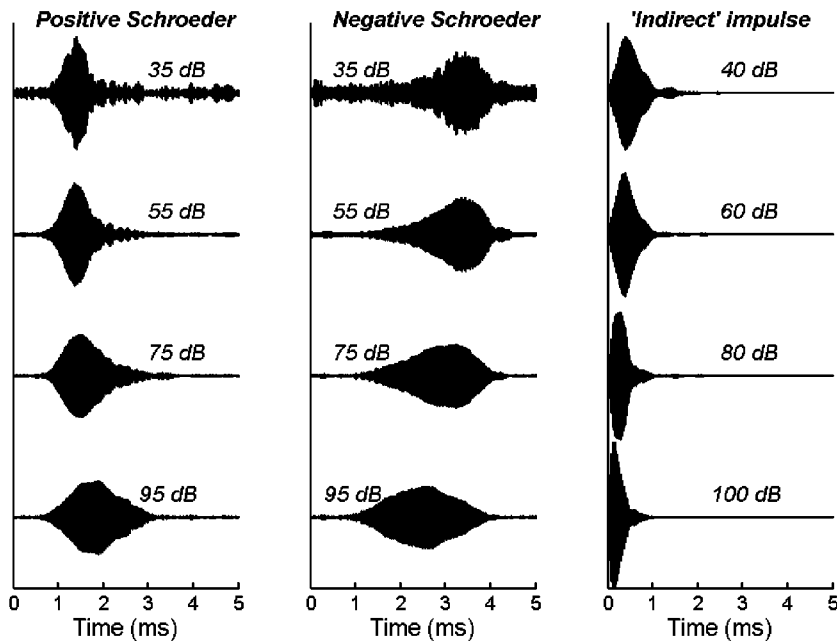


FIG. 5. As Fig. 4, for a different experiment.

the form of “spindles” of which the slowly decaying part points to the right (i.e., follows the response peak) for responses to +Schr signals, and to the left (preceding the peak) for responses to –Schr signals. Note that the relative amplitude of this slowly decaying part of the response steadily increases with input level, particularly for the –Schr stimulus. Thus, with increasing level, the response to the –Schr stimulus is more and more “filled up” within a period. Responses to the +Schr stimuli also show some of this “filling” with level, but more nearly retain their low-level pattern, a peak region followed by a long period of “silence.” Input level also influences the temporal locations of the response peaks. Similar to the pattern just described, the peak moves to the right for +Schr stimuli and to the left for –Schr complexes.

The level-dependent changes in the response patterns for the +Schr and –Schr stimuli (peak shifts and filling on one side of the peak) are again consistent with a greater influence of the low-frequency parts of the input on responses as levels increase (recall that the low-frequency parts of the stimulus signal occur late within each period for the +Schr stimuli and early for the –Schr complexes). The peak shifts and partial filling of the response period with level are among the effects that should be captured by the level-dependent changes in the indirect impulse responses (Fig. 2) in order for predictions based on the impulse data to provide a close match to measured responses for the Schroeder-phase stimuli. This modeling is described next.

IV. PREDICTION OF RESPONSES TO HARMONIC STIMULI

In a linear system, the impulse response is invariant with input level and allows accurate prediction of responses to arbitrary stimuli. In the nonlinear cochlea, indirect impulse responses show large changes in magnitude spectra and small changes in phase with level, and may not necessarily

predict responses to other inputs well. To examine the accuracy of prediction, *measured* responses to +Schr and –Schr stimuli are to be compared to *predicted* responses based on the indirect impulse response data. Predicted responses are determined by filtering the stimulus waveforms using filter characteristics derived from indirect impulse responses. The first issue to address is to assess *the most appropriate stimulus level* for the impulse response. Let us assume that in the cochlea, outer hair cells (OHCs) produce a place-frequency-specific enhancement of the response and that physiologic saturation in OHCs is the (sole) cause of cochlear nonlinearity. In de Boer and Nuttall (2000), it is shown that the shape of the indirect impulse response is fairly accurately determined by the *average degree of saturation* of OHCs for the noise stimulus employed. In the paper cited, the correspondence is shown for noise stimuli and indirect impulse responses, in fact, for stimuli and responses that are regular in the stochastic sense, and certainly not peaky in their waveforms. For such stimuli the average degree of saturation directly depends on the level of the stimulus, and on nothing else. The close correspondence between direct and indirect impulse responses, mentioned in the Introduction, indicates that the stimulus or the response being peaky or nonpeaky is not an important condition. In a recent paper, de Boer and Nuttall (2002) have shown that the correspondence is also true for tones versus noise. That the stimulus has a narrow spectrum is, therefore, not a constraint either. For all these reasons, we may expect that response prediction will also work in the case of Schroeder stimuli.

Prediction is carried out by convolving the stimulus waveform with the appropriate indirect impulse response. A point to be noted is that our indirect impulse responses are compensated for the response of the stapes. The same has to be done for the measured responses to Schroeder stimuli, otherwise, the prediction will not work. The upper portion of Fig. 6 shows *measured* and *predicted* response waveforms for a 35 dB SPL +Schr stimulus and the lower part of the

Experiment 20026: Positive Schroeder

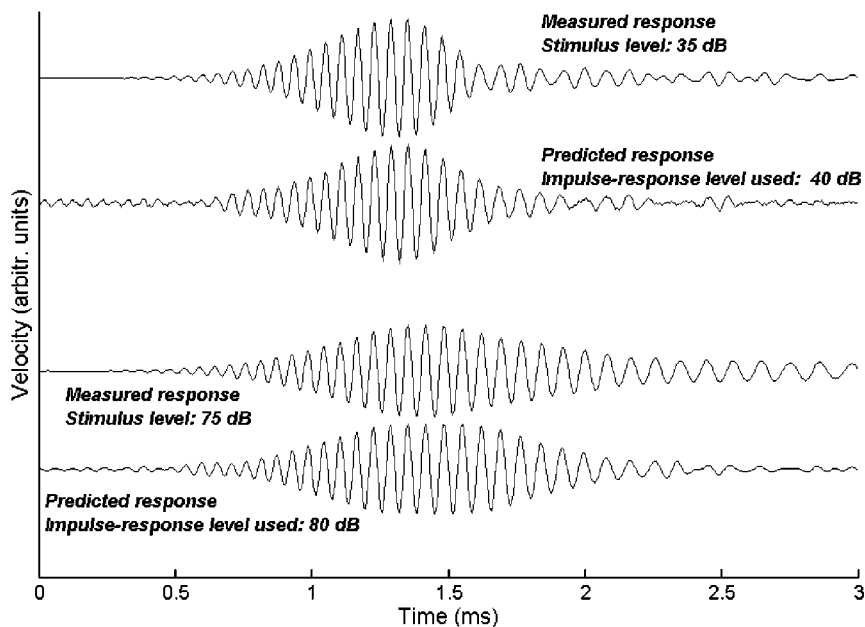


FIG. 6. Typical measured BM responses to a positive Schroeder stimulus and predicted response waveform for that signal based on indirect impulse responses. Upper waveform pair shows measured and predicted responses at low stimulus level; lower pair shows high stimulus level. Note the fairly accurate reproduction of envelope waveform and frequency glide.

figure shows the same data for a 75 dB SPL stimulus. The presentation levels for Schroeder stimuli and noise are closely matched, assuming that this leads to a similar average degree of saturation. Note that the abscissa scale has been shortened to go from 0 to 3 ms. It is clear that measured and predicted responses are very similar: Pearson correlation coefficients between measured and predicted waveforms for both the 35- and 75-dB responses are approximately 0.96.

Figure 6 shows details of both envelope and fine structure of the measured and predicted waveforms. A Lissajous figure, in which all values from the predicted response waveform are plotted against corresponding values in the measured response, gives a second view of the relation between measured and predicted signals. Figure 7 shows a set of such Lissajous figures. In the vertical direction, the stimulus level

in the panels varies from 35 to 95 dB SPL, in steps of 20 dB. In the horizontal direction it is the stimulus level of the indirect impulse response with which the response is predicted that is varying, and this level varies in steps of 10 dB. Along two of the rising diagonals of the figure (the one beginning in the lower left-hand corner and the one immediately to its right) the impulse level used in prediction differs by only 5 dB from the actual response level. The remaining diagonals involve differences of 15, 25, or 35 dB between the indirect impulse (predictor) and the response level. In each panel, waveform values from actual responses are plotted as a function of predicted values; a 45-degree line within a given panel would represent perfect prediction. Pearson r values correlating predicted and actual values are shown in each panel. In general, correlations were high (>0.9) when pre-

Experiment 19916: Positive Schroeder

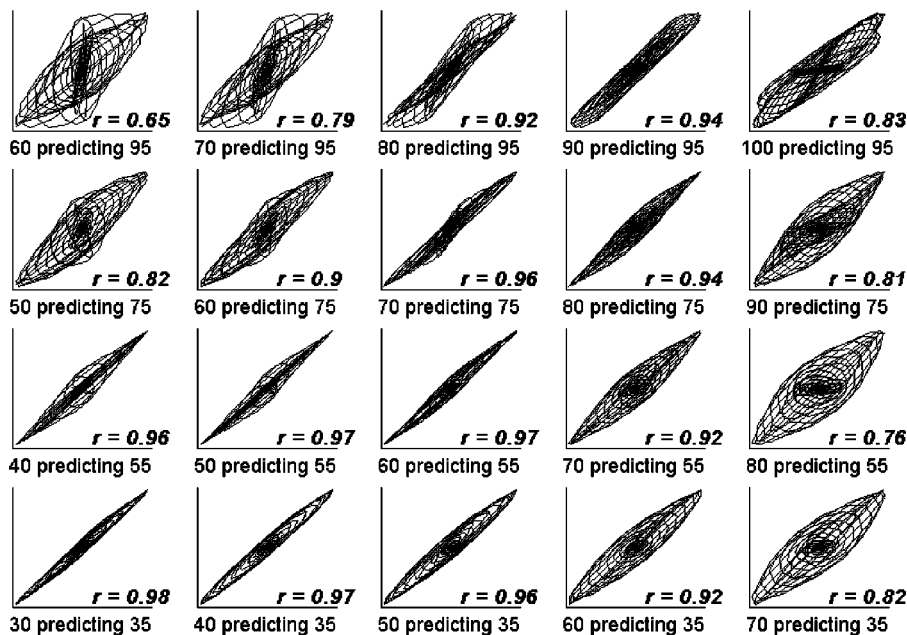


FIG. 7. (Experiment 19916). Measured and predicted responses for positive Schroeder stimuli. Lissajous figures of predicted response (horizontal) versus measured response (vertical). All signals are normalized with respect to 1.05 times their maximal values and the scales go from -1 to +1. In one row, predictions are done with different stimulus levels of the (indirect) impulse response, and the stimulus level of the response is constant. The abscissa label of every panel tells the level of the impulse response used for prediction, and the level of the response to be predicted. All levels are in dB SPL between 10 and 20 kHz.

Experiment 20026: Positive Schroeder

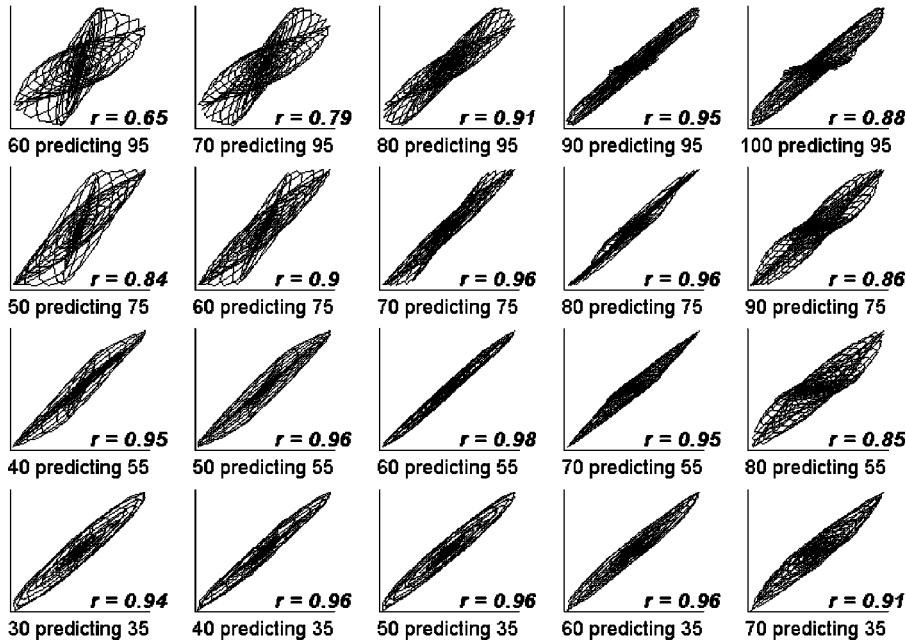


FIG. 8. (Experiment 20026). Measured and predicted responses to positive Schroeder stimuli. Layout as Fig. 7.

dictions and measured responses were closely matched in level, and were found to decrease steadily as the difference in level between the impulse and harmonic stimuli increased. As suggested by the high Pearson correlation coefficients along the two central diagonals of Fig. 7, and as directly indicated by the measured and predicted responses shown in Fig. 6, the prediction procedure accurately recovered both the peak shifts and increased filling of the response period with increasing level.

It should be realized that a correlation coefficient is not necessarily the best descriptor of the similarity in shape of two waveforms because it intrinsically weighs the larger amplitudes quadratically. Obviously, the variations in response

to Schroeder-type stimuli are complex and subtle. On the other hand, a “narrow” Lissajous figure means that variations in envelope are simulated well. We also verified that, wherever the Lissajous figures are narrow, the intrinsic frequency modulation of the waveform (the glide) is well predicted. This means that the fine structure is preserved, too. Figure 8 shows Lissajous figures for another experiment. Across experiments, Lissajous figures tended to show the best correspondence when predictor and response levels differed by only 5 dB. Figures 7 and 8 show predictions and measured responses to +Schr stimuli. Figure 9 shows an example of predictions for -Schr signals. Since it is similar to the earlier figures and does not lead to different conclu-

Experiment 19916: Negative Schroeder

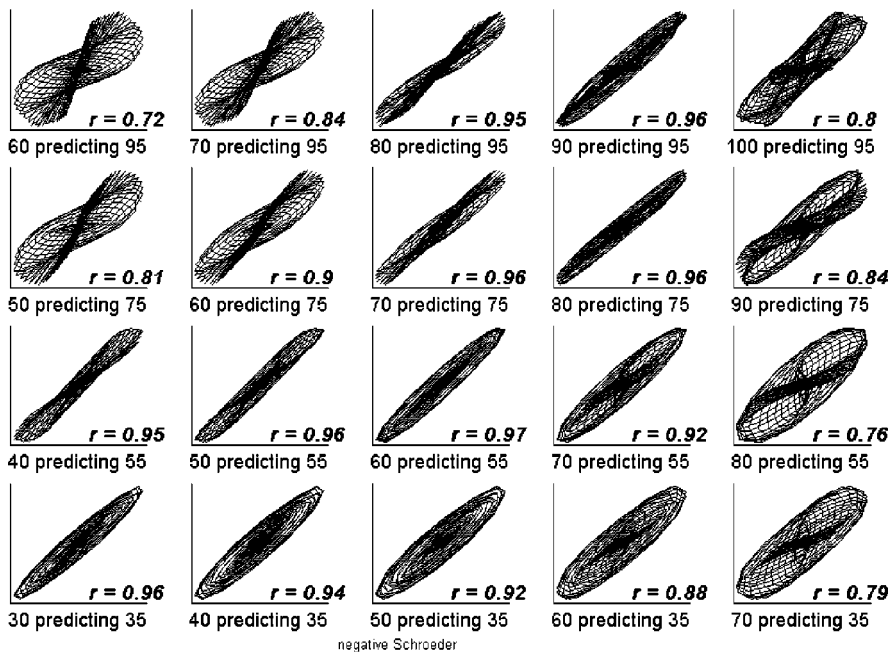


FIG. 9. (Experiment 19916). Measured and predicted responses for negative Schroeder stimuli. Layout as Fig. 7.

sions, we refrain from presenting figures for $-Schr$ signals for other experiments.

V. DISCUSSION

In the present study, BM velocity response envelopes in guinea pigs were peakier for $+Schr$ than $-Schr$ complexes, particularly at low input levels (see Figs. 4 and 5). As described earlier, peaky responses to $+Schr$ complexes are consistent with (partial) cancellation of the high-to-low frequency glide of the $+Schr$ signal (or equivalently, positive curvature in the stimulus phase structure) by the low-to-high frequency glide (or negative curvature in response phase) inherent to basal cochlear mechanics. The indirect impulse responses allowed accurate prediction of responses to the two Schroeder-phase complexes over a 60 dB input range. The results of this analysis are discussed more fully below, along with a consideration of how spatial dispersion of frequencies during traveling-wave propagation may account for certain aspects of the data, and some implications of these data for previously reported psychophysical results.

A. Predicting response to Schroeder-phase complexes based on indirect impulse data

At low stimulation levels, prediction of responses is straightforward since we may assume the cochlea to be operating linearly. We have employed exactly the same technique for prediction at higher stimulus levels, with the only modification that the cochlear transfer function is taken from the indirect impulse response determined at an appropriate stimulus level. The predictions proved to be quite good, at least when levels were closely matched. Lissajous figures demonstrate the agreement clearly. We verified in a separate test that not only the envelope modulation of the response is predicted well but also the fine structure. The reason why Lissajous figures are not all like straight lines probably lies in slow variations of the phase that are not captured in the prediction. The nonlinear processes in the cochlea apparently do not contain subprocesses that are strongly frequency dependent, or are disrupting temporal relations, and we are fully justified in continuing an analysis as if the cochlea is linear at any one level as we employed in the experiments. The fundamental concept underlying the use of noise stimuli and spectral analysis in a nonlinear system as the cochlea lies in the EQ-NL theorem (de Boer, 1997). This theorem prescribes the conditions to be met by the system for this quasilinear analysis to be justified. As far as we know, the cochlea can well be modeled by such a system.

Consider Fig. 11 in the Appendix. Thick lines in the two panels of the figure show the course of the (unwrapped) phase for a positive and a negative Schroeder stimulus, respectively. The figure shows that the sampling of frequencies and the unwrapping of phase that have taken place do not disrupt the size and polarity of the phase curvature (the second derivative). The phase of the cochlear transfer function has to be added to the phase of the stimulus and this summed phase function always has a negative curvature. That curvature is largest in the frequency region of the response peak. Hence, its effect on the response will be large whenever that frequency region is important. In other words, at low stimu-

lus levels, where the response has a sharp spectrum centered at the CF, the phase modification will be large. This situation is depicted by the thin curve in the upper panel of Fig. 11, the positive phase curvature is *diminished* locally, i.e., in the frequency region of the peak (the thick bar on the abscissa).

For $-Schr$ stimuli (lower panel, Fig. 11) at low stimulus levels the effect on the response phase is to *enhance* the curvature in that frequency region. Figure 12 of the Appendix shows prototype waveforms for these two cases. In both figures the curvature of the phase is taken as constant. In the upper waveform it is small and positive, and in the lower waveform, large and negative. In the construction of that figure the amplitude spectra were stylized (see the legend); they were not meant to correspond to cochlear responses. Nevertheless, an important property can be deduced from the figure, a property that can also be discerned in actual responses. That property is the following: signals with a restricted spectrum and a *large* phase curvature have a *long* waveform (a long “spindle”). Conversely, signals with a *small* phase curvature have a *short* waveform.

At higher stimulus levels the region of large phase curvature in the response becomes less important so that the curvature due to the Schroeder stimulus signal dominates the response phase. Consequently, the response waveforms tend to show the character of the prototype response of the lower waveform in Fig. 12. The fact that the actual spectrum of the response is not the stylized one used for that particular figure causes the spindles of both the measured and predicted responses to deviate from the prototypes. Hence, the pronounced effects of stimulus level. In particular, with increasing level, BM responses decrease less in modulation for $-Schr$ than for $+Schr$ stimuli. This reasoning also shows why the predictions depicted by the Lissajous figures fail when the level difference is large. In that case the weighting of the spectral components is way off, and a good prediction cannot be reached. The Lissajous procedure is very sensitive in this respect.

Actually, even at low levels the compensation of the Schroeder phase curvature is not complete because the narrowest indirect impulse responses in Figs. 4 and 5 are peakier than the $+Schr$ responses. It may be asked: are these indirect impulse responses the peakiest possible responses in the cochlea? The answer is no. It is possible to construct a hypothetical stimulus that precisely compensates for the cochlear glide. For this purpose the *amplitude* frequency spectrum of a Schroeder stimulus is taken as the spectral amplitude [see Fig. 1(c)]. This amplitude is endowed with the opposite of the phase spectrum of the indirect impulse response. The resulting signal is noncausal (i.e., nonzero portions of the signal precede time zero). If such a signal could be presented to the cochlea, the response (also noncausal) would have a constant phase for all component frequencies involved. Figure 10 shows a typical high-level indirect impulse response and the predicted, *artificial response* to the hypothetical stimulus. The latter response is the peakiest that could ever be obtained in this cochlear region, given the amplitudes in the frequency spectrum.² The effective duration of even the peakiest impulse response of the cochlea is larger than the duration of this hypothetical response.

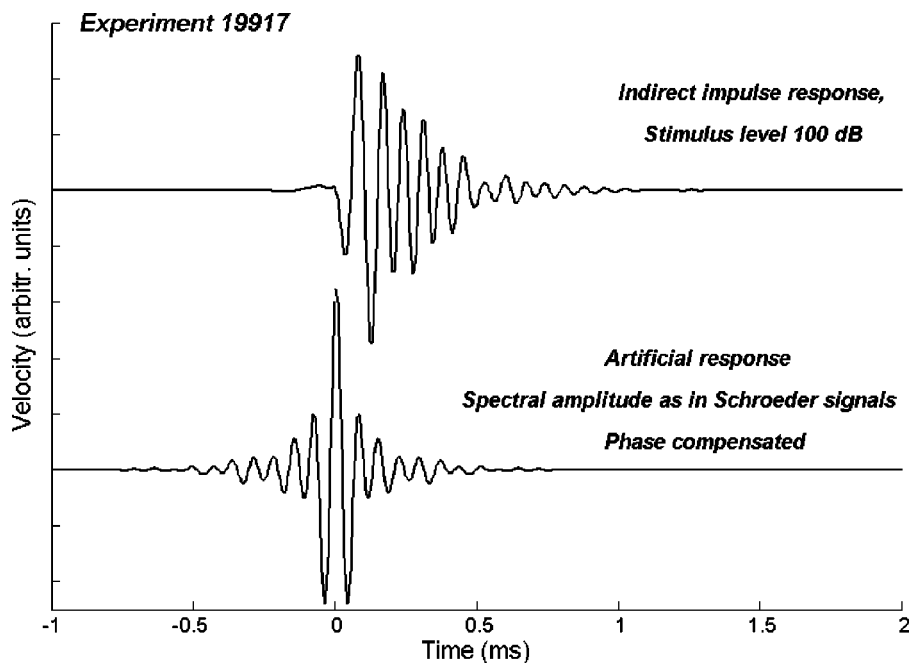


FIG. 10. The “narrowest response of the cochlea.” Upper waveform: high-level indirect impulse response (stimulus level 100 dB SPL for the 10–20 kHz octave band). Lower waveform: an artificial response derived from a spectrum of which the amplitude is the product of the spectral amplitude of a Schroeder-type signal and the amplitude of the corresponding (high-level) cochlear transfer function, and the phase is zero.

B. Effects of traveling wave dispersion on response envelopes

The reasoning contained in the preceding paragraphs focuses on the frequency domain and how phase curvature in the stimulus spectrum and the BM transfer function (as derived from the indirect impulse response) combine to influence the shape of the measured response. The origin of phase curvature in the intrinsic BM response appears to lie in *dispersion* of waves traveling in the cochlea. Spatial dispersion can be understood in terms of a (mechanical) model of the cochlea. Such a model generally has the shape of an elongated cavity filled with fluid. The fluid has two outlets, the round window and the oval window (in which the stapes fits). The fluid column is divided into two parts separated by the “cochlear partition,” a long structure representing the mechanics of the basilar membrane and the organ of Corti. In the model dispersion arises, first, from inhomogeneity of the mechanics of the cochlear partition (de Boer, 1996, Sec. 4), and, second, from hydromechanical properties of the fluid wave. That wave starts out at the stapes as a “long” or “shallow-channel” wave (the wavelength is large compared to the cross-sectional diameter of the fluid channel), and gradually turns into a “short” or “deep-channel” wave (the wavelength is becoming shorter and shorter until it is short compared to the cross-sectional diameter of the fluid channel). A more detailed description of the latter process can be found in Patuzzi (1996) and a theoretical account in de Boer (1996, Sec. 5). The net result of these processes is that low-frequency waves travel faster and arrive earlier at the peak region than high-frequency waves (Shera, 2001). This applies in particular to the basal part of the cochlea. The immediate consequence of this dispersion is found in phase curvature in the frequency domain.

The phase results derived from the indirect impulse data (Sec. III A) agree with response measures reported by others (Sellick *et al.*, 1983; Ruggero *et al.*, 1997) in showing clear evidence of negative phase curvature in the tip region (be-

ginning about half an octave below CF). However, in the low-frequency (tail) region, phase plots—on a linear frequency scale—show little or no curvature, consistent with the notion that these frequencies propagate nondispersively (at a similar rate for all frequencies). With increases in level, linear response growth in low-frequency (“tail”) regions combined with compressive (i.e., less than linear) growth in high-frequency “tips” leads to a lowering of the BF and an increase in the relative influence of tail regions on the overall response. Given that components with low frequencies propagate at a nearly constant rate, they arrive essentially unchanged at the measurement location (with the exception of some added, constant delay). Now, consider the changes in response envelopes with level shown for the Schroeder-phase signals and the indirect impulse responses in Figs. 4 and 5. In each experiment and for all three stimulus types, increases in level lead to response envelopes that more and more closely resemble the envelopes of the external (or indirectly modeled) input stimuli. That is, response envelopes become flatter for the two Schroeder-phase signals, and peakier (more impulsive) in the case of the indirect impulse data.

Nondispersive propagation of low frequencies is found in the apex of the cochlea where phase by frequency plots for low-frequency components approximate straight lines, indicating propagation delays which are independent of frequency. Consequently, in the apex, the low-to-high frequency glide present in basal regions is not observed (Rhode and Cooper, 1996; Khanna and Hao, 1999; Hemmert *et al.*, 2000; Zinn *et al.*, 2000).

C. Implication for psychophysics

In psychophysical experiments, +Schr complexes are often less effective maskers than corresponding –Schr complexes (Smith *et al.*, 1986; Kohlrausch and Sander, 1995; Carlyon and Datta, 1997a,b; Summers and Leek, 1998; Sum-

mers, 2000; Oxenham and Dau, 2001a,b). Beginning with Smith *et al.* (1986), these masking differences have been interpreted as being linked to the envelope characteristics of BM responses to the two maskers and the idea that a more modulated (peakier) internal response will be produced by an appropriately selected +Schr complex than by a time-reversed (−Schr) version of that stimulus. By these accounts, reduced masking effectiveness for +Schr stimuli is due to probe signal detection during low-amplitude (“quiet”) regions between brief high-amplitude peaks in the internal response to this masker. These differences in the internal response envelopes for +Schr and −Schr complexes have now been verified physiologically, both in chinchillas (Recio and Rhode, 2000) and guinea pigs (present data). In addition, the present data show that the modulation differences in BM responses to +Schr and −Schr stimuli are reduced at high presentation levels where the influence of curvature in the BM phase response is reduced, particularly in the BF region. Greater similarity of response envelopes for the two stimuli at high levels is also consistent with the masking literature: the effectiveness of +Schr and −Schr maskers is very similar at high presentation levels (Summers and Leek, 1998; Summers, 2000).

The masking results cited in the previous paragraph all involved human listeners. To our knowledge, other mammalian species have not been tested psychophysically with Schroeder-phase (or closely related) maskers. However, several species of birds have been tested and show very different results from humans (Leek *et al.*, 2000; Dooling *et al.*, 2001). In three different avian species, +Schr maskers were as effective, or slightly more effective, than −Schr complexes. These results suggest that the negative phase curvature in the BM response observed in mammals may not be present in birds. Although data on BM response in birds are limited, Gummer *et al.* (1987) reported results indicating slight *positive* curvature in BM phase response for pigeons.

The current results demonstrate clear differences in BM response envelopes for +Schr and −Schr complexes composed of identical harmonic components and with extremely similar (very flat) external envelopes. Negative curvature in the intrinsic BM phase response tends to partially cancel the positive phase curvature of +Schr stimuli, producing greater modulation in the BM response than is seen for −Schr stimuli. Responses to the two complexes become increasingly similar as input level increases. The results point out an aspect of cochlear nonlinearity which has previously received little attention. That is, as levels increase, phase curvature in the BF region tends to decrease dramatically. Our results show how the level-dependent changes in response characteristics for the Schroeder-phase stimuli are directly related to and can be determined quantitatively from cochlear nonlinearity.

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private views of the authors and are not to be construed as official or as reflecting the views of the Department of the Army or the Department of Defense.

APPENDIX: UNWRAPPING THE PHASE OF SCHROEDER SIGNALS

Equation (1) leads to phase values that eventually exceed the limits $-\pi$ and $+\pi$ so that every phase value has to be “unwrapped” in order to be interpreted. Take, for example, the +Schr stimulus, N_c equal to 100, and n equal to 10. The phase is 0.9π , and for the next value of n it crosses the π boundary and becomes 1.1π , which is equivalent to -0.9π . In the experiments it is the *waveform* of stimulus and response that is recorded, and we wish to derive the relation between these two by using the frequency *spectrum*. For this purpose we apply a Fourier transform to the stimulus and to the recorded waveforms. In the Fourier spectra of the recorded signals all phase values then appear within the limits $-\pi$ and $+\pi$, and the phase functions have to be unwrapped. This unwrapping has to be done in such a way that for the *stimulus* signal the phase function appears (more or less) in the form of Eq. (1), and that a similar form of a monotonically increasing or decreasing function of frequency appears for the *response* phase. Unfortunately, this cannot be done in the ideal way. Figure 11 illustrates the result of the unwrapping procedure for typical signals used in the present work. Consider panel (a). The *thick curve* is the unwrapped phase curve for the +Schr stimulus. For frequencies below 10 kHz this curve follows the form of Eq. (1), but above that frequency the slope of the function suddenly becomes negative. In fact, above that frequency the index n is higher than 50, the quantum steps in the original phase function are larger than π , and the unwrapping routine is unable to follow them and to reconstruct the original phase function accurately. Actually, with every next step of the index n one step of 2π is missed in the unwrapped phase, and the result of unwrapping is a function with negative slope. Note, however, that the *second derivative* of the phase function is not affected (with the exception of one point just prior to where the function reverses direction). Why this is so needs some explanation. To form the second derivative, *three* successive phase values ($\theta_1, \theta_2, \theta_3$) are needed. The first and the third are added, and two times the central one is subtracted. That in each step of the index n an additional step of 2π is missed does not influence the result for the second derivative. That is, for $x = 0, 1, 2, 3, \dots$,

$$\theta_1 - 2\theta_2 + \theta_3 = (\theta_1 - 2\pi(x)) - (\theta_2 - 2\pi(x+1)) + (\theta_3 - 2\pi(x+2)).$$

Therefore, the second derivative, i.e., the *curvature* of the phase, is retained. The *thin curve* in panel (a) shows the result of unwrapping the phase of a typical response signal. This curve confirms that the second derivative is not materially affected by the unavoidable errors in the data. Panel (b) of Fig. 11, *thick curve*, shows the corresponding situation for the −Schr stimulus. The *thin line* shows the unwrapped phase for a typical experiment, and, again, the unwrapping

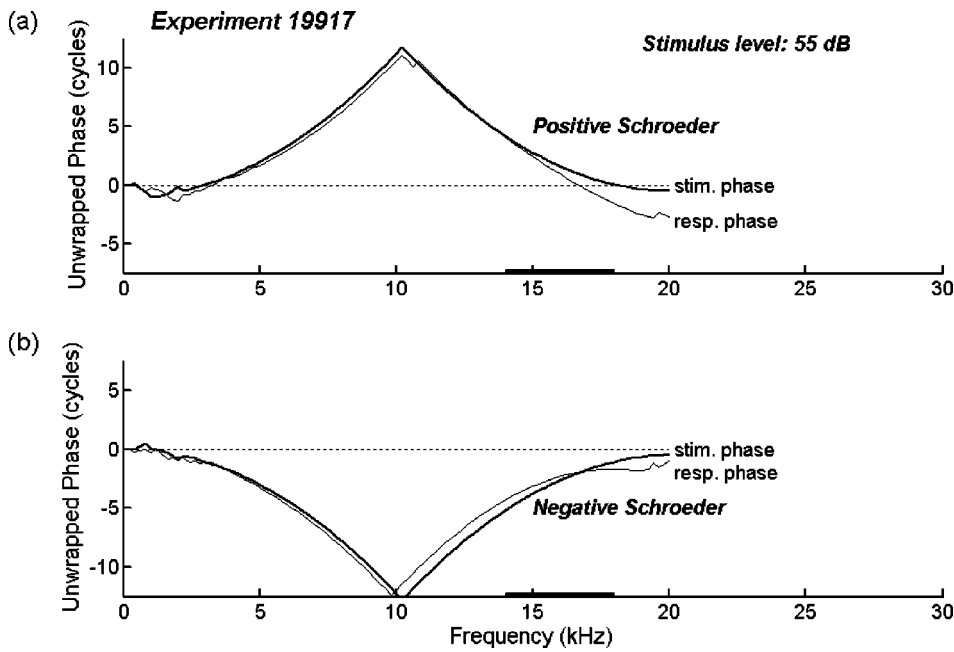


FIG. 11. Unwrapped phase, as a function of frequency. Thick part of the abscissa indicates the region of the response peak (14 to 18 kHz). Thick curve: phase of Schroeder stimulus, thin curve: phase of response. Panel A: positive Schroeder, panel B: negative Schroeder signal. Note how in the upper panel the *phase curvature* is diminished in the peak region, and in the lower panel it is increased in the same region.

routine is accurate enough to reveal the true estimate of the phase curvature.

In Sec. IV it is shown that prediction of responses as if the cochlea is a linear device is pretty accurate. In terms of complex spectra, the spectrum of the stimulus signal is simply multiplied by the cochlear transfer function—which is the spectrum of the cochlear (indirect) impulse response. In this multiplication the phase values are added, and so are the second derivatives. Consider panel (a) of Fig. 11 again. The phase curvature of the spectrum corresponding to the impulse response is negative in the peak region but smaller in magnitude than the positive one corresponding to the stimulus. Hence, the resulting response phase still has a positive curvature but it is smaller than that of the stimulus, and the curvature is smallest in the peak region. Panel (b) shows the corresponding situation for a $-$ Schr signal. In this case the stimulus signal has negative phase curvature and this be-

comes larger in magnitude in the peak region when the phase of the cochlear transfer function is added.

Figure 12 illustrates the influence of phase curvature in the (linear) frequency domain on the temporal waveform. The figure shows waveforms of signals with a restricted spectrum (see the legend) and phase values that are quadratic functions of frequency. In the waveform plotted in the upper portion of the figure, the phase curvature over the entire frequency range is small and positive [corresponding to the situation in the peak region of panel (a) of Fig. 11]. The waveform has a negative (downward) glide and a short duration, i.e., it is “peaky,” as we call it in the main text. In contrast, phase curvature for the waveform in the lower part of the figure is negative, constant, but four times larger (see the legend). Consequently, the waveform has a long duration. Furthermore, it has a positive (upward) glide. Note the typical “spindle” form of the two waveform envelopes; note also

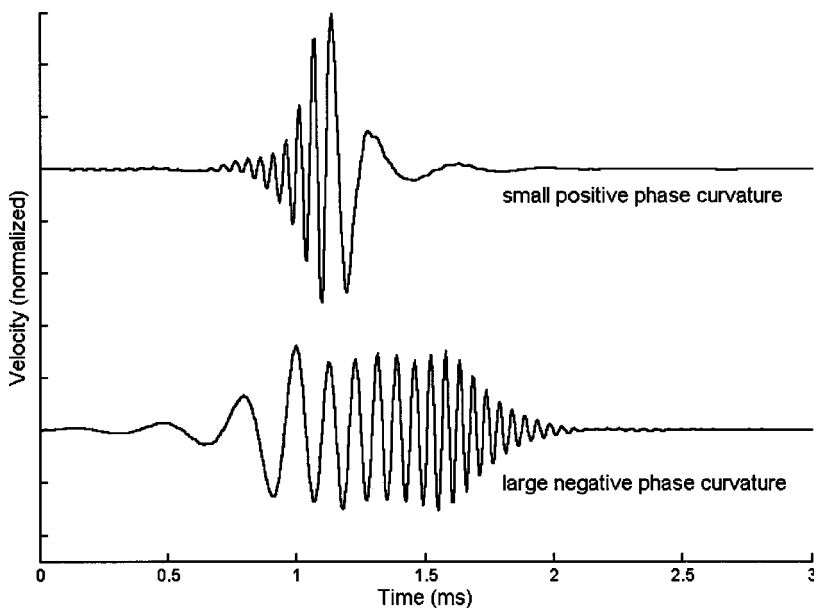


FIG. 12. Waveforms of bandlimited signals of which the phase $\varphi(f)$ of the components is a quadratic function of frequency f . The spectrum is restricted from 2.5 to 22.5 kHz, has constant amplitude, but the outer edges are rounded off. Upper waveform: signal with a positive sign in the phase function. Phase follows (apart from a delay term): $\varphi(f) = +(f/(100f_0))^2$, where f_0 is the sampling frequency (208 kHz). Lower waveform: signal with positive sign in the phase function; the coefficient of the quadratic term is four times larger than in panel (a), the phase follows: $\varphi(f) = -(f/(50f_0))^2$. Note the inversion of the glide in the waveform, and of the direction of the spindle.

that in the upper waveform, the spindle points to the left and, in the lower wave, to the right.

¹The indirect impulse responses were derived from “composite-spectrum files” of which low- and high-frequency parts were acquired separately (de Boer and Nuttall, 1999). The level of the noise then formally refers to the high-frequency part, which was one octave wide.

²To avoid considering the presentation of a noncausal signal to the cochlea, a time-shifted (nearly causal) version of the same signal may be substituted. This signal would produce a time-shifted, but otherwise identical response.

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