Iterated intracochlear reflection shapes the envelopes of basilar-membrane click responses

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Multiple internal reflection of cochlear traveling waves has been argued to provide a plausible explanation for the waxing and waning and other temporal structures often exhibited by the envelopes of basilar-membrane (BM) and auditory-nerve responses to acoustic clicks. However, a recent theoretical analysis of a BM click response measured in chinchilla concludes that the waveform cannot have arisen via any equal, repetitive process, such as iterated intracochlear reflection [Wit and Bell (2015), *J. Acoust. Soc. Am.* **138**, 94–96]. Reanalysis of the waveform contradicts this conclusion. The measured BM click response is used to derive the frequency-domain transfer function characterizing every iteration of the loop. The selfsame transfer function that yields waxing and waning of the BM click response also captures the spectral features of ear-canal stimulus-frequency otoacoustic emissions measured in the same animal, consistent with the predictions of multiple internal reflection. Small shifts in transfer-function phase simulate results at different measurement locations and reproduce the heterogeneity of BM click response envelopes observed experimentally.

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I. INTRODUCTION

The envelopes of basilar-membrane and auditory-nerve responses to low-level acoustic clicks often exhibit striking temporal structures, including multiple sequential bursts or lobes (Recio *et al.*, 1998; Lin and Guinan, 2000; Rhode, 2007; Guinan and Cooper, 2008). Figure 1 provides an example measured in the motion of the basilar membrane (BM) at low sound levels (Shera and Cooper, 2013). The figure shows BM displacement in a sensitive chinchilla at a measurement location and click level where the lobes appear especially regular and distinct. Reminiscent of the beating between resonators with similar natural frequencies, the temporal structure of the BM response envelope has been hypothesized to arise from interactions among coupled nonlinear oscillators (Zweig, 2003; Aranyosi, 2006) or between multiple vibrational modes of the organ of Corti (Lin and Guinan, 2000, 2004). As an alternative to explanations that ascribe the beating pattern to local resonators interacting at the site of measurement, Shera and Cooper (2013) argue—on the basis of a correlate observed in ear-canal pressure—that waxing and waning of BM response envelopes is a consequence of global interference patterns arising from multiple internal reflection of waves traveling within the cochlea.

In a recent paper, Wit and Bell (2015) contribute to the discussion by asking whether the series of bursts constituting the BM click response are consistent with an origin involving any sort of “equal, repetitive process.” Although their analysis is more general, the repetitive process they have in mind is precisely the multiple-internal-reflection model proposed by Shera and Cooper (2013). In this model, the bursts arise as the pressure waves that drive the BM echo back and

forth between the stapes and the site of measurement. Wave propagation and reflection combine to form an intracochlear feedback loop in which the “output” of one iteration (e.g., the wave energy evident in a particular burst) becomes the input for the next (see Fig. 2). Each burst appears as the echo of the one preceding it, and each traversal of the loop represents a cycle of round-trip wave propagation and reflection. Since cochlear traveling waves are dispersive, and wave scattering along the partition is presumably distributed in both space and time, the duration of each burst can exceed the mean round-trip travel time, and the bursts will generally partially overlap. The bursting then appears most pronounced when adjacent echoes combine out of phase and cancel during the period of overlap, creating distinct lobes in the waveform envelope. In other cases, also observed experimentally (e.g., Recio *et al.*, 1998, Fig. 4), the click response may merely be prolonged, providing little hint of an underlying repetitive process. Although Shera and Cooper (2013) argue that multiple internal reflection provides a plausible explanation for the waxing and waning evident in Fig. 1, Wit and Bell (2015) perform a close analysis of the measured waveform and conclude that the BM click response cannot have arisen via any such iterative process.

In paraphrase, their argument runs as follows. Wit and Bell (2015) model the BM click response $d_{\text{BM}}(t)$ on the analyzed time interval as the sum of $N = 5$ separate bursts, $b_n(t)$, and a residue, $\delta(t)$. Thus,

$$d_{\text{BM}}(t) = \sum_{n=1}^N b_n(t) + \delta(t). \quad (1)$$

The residue accounts both for measurement noise and for possible inadequacies of the model. Taking Fourier transforms, $\mathcal{F}$, yields the corresponding frequency domain equation

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FIG. 1. Waxing and waning in the basilar-membrane click response. (A) Basilar-membrane displacement produced by a low-level acoustic click as measured near the 7 kHz place in a sensitive chinchilla (Shera and Cooper, 2013). (B) Delayed bursts or echoes in the time-domain waveform generally appear as quasiperiodic ripples in the corresponding Fourier spectrum (solid black line). The dashed gray line shows a smoothed spectrum representing the transform of the initial burst described in the text.

$$D_{\text{BM}}(f) = \sum_{n=1}^N B_n(f) + \Delta(f), \quad (2)$$

where symbols in uppercase denote the Fourier transforms of variables in lowercase [e.g., $B_n(f) \equiv \mathcal{F}\{b_n(t)\}$]. The transformations that convert one burst into the next can then be found by computing the transfer functions ${}^nH_{n+1}(f) \equiv B_{n+1}(f)/B_n(f)$ representing the ratios of successive terms. When rewritten using the ${}^nH_{n+1}$, Eq. (2) becomes

$$D_{\text{BM}} = B_1 + B_1 {}^1H_2 + \cdots + B_1 {}^1H_2 {}^2H_3 \cdots {}^{N-1}H_N + \Delta, \quad (3)$$

$$= B_1 \left(1 + \sum_{n=2}^N \prod_{m=1}^{n-1} {}^mH_{m+1} \right) + \Delta. \quad (4)$$

If the measured bursts arise iteratively via repeated application of the same process or transformation, then the

FIG. 2. Multiple internal reflection represented as an iterated loop. Once initiated by an external click stimulus, the repetitive cycle of round-trip wave propagation and reflection within the cochlea produces a series of bursts measurable both in basilar-membrane motion and in ear-canal pressure. Although the diagram indicates that reverse waves arise by “scattering,” consistent with coherent reflection theory, an analogous loop presumably applies for any other process capable of generating reverse-traveling waves.

${}^nH_{n+1}$ should all be equal. Wit and Bell (2015) test for this equality by modeling the higher-order bursts using Gaussian-shaped tone pips and computing the resulting transfer functions. (Their tacit assumptions here are that the system is time-invariant and that BM motion remains small enough that nonlinearities in the mechanics can be neglected.) They find that the function 1H_2 describing the transformation of burst 1 into burst 2 differs markedly from the functions describing the transformation of subsequent bursts (i.e., 2H_3 , 3H_4 , and so on). For example, whereas the transfer function 1H_2 is sharply bandpass in form, the others are all-pass (i.e., have constant magnitudes). Wit and Bell (2015) conclude that multiple internal reflection—or, indeed, any iterated process—cannot fully account for the features of the measured impulse response. Were it to prove compelling, the analysis by Wit and Bell (2015) would support non-iterative explanations for waxing and waning, such as those involving the interaction of local resonators.

The conclusions of Wit and Bell (2015) are undercut, however, by a circularity inherent in the argument. Their procedure for estimating the transfer functions ${}^mH_{m+1}$ begins with the observation that “the first burst ... has a complex structure but the following [four] bursts are more regular.” Accordingly, at times after the initial burst they model the waveform as the sum of four tone pips, all with the same functional form (namely, a sinusoid with a Gaussian envelope) and parameters (a fixed oscillation frequency and envelope duration and, from burst to burst, a constant relative attenuation, phase shift, and delay). Although this representation yields a surprisingly good fit to the waveform, especially considering the small number of parameters, the model cannot meaningfully probe the central hypothesis. Indeed, the adopted model structure guarantees at the outset that the transfer functions 2H_3 , 3H_4 , and 4H_5 all have the same predetermined form (all-pass filters with constant magnitude and linear phase) and that the transfer function 1H_2 , which must account for the “complex structure” of the first burst, will necessarily be different.

The conclusions of Wit and Bell (2015) are therefore entirely preordained by their modeling approach, and the question they ask remains unanswered: Can a single transfer function—a single, repetitive process—reproduce the form of all bursts? Does the complex structure evident in the initial burst really recede into regularity, as the model assumes, or has it merely been relegated to the model residue? Answers to these questions have important implications for understanding the physical mechanisms responsible for shaping the cochlea’s mechanical response to sound.

II. FINDING THE ITERATED PROCESS

To proceed without begging the question, we recast the analysis by Wit and Bell (2015) in a more model independent way. When the transfer functions are assumed equal, so that ${}^nH_{n+1} = H$, Eq. (4) for D_{BM} reduces to a polynomial in H ,

$$D_{\text{BM}} = B_1 \left(1 + \sum_{n=1}^{N-1} H^n \right) + \Delta. \quad (5)$$

Given an estimate of the spectrum, B_1 , of the initial burst, the transfer function H can therefore be found by solving the complex quartic equation $q(H) = 0$, where

$$q(H) = H^4 + H^3 + H^2 + H + (1 - D_{\text{BM}}/B_1), \quad (6)$$

derived from Eq. (5) with $N=5$ by requiring that $\Delta=0$. At each frequency, the fundamental theorem of algebra (Palka, 1991, Theorem 3.8) guarantees that Eq. (6) has four roots ($H_{1,2,3,4}$), obtainable numerically or in closed form.

Figure 3 shows the transfer function $H(f)$ found by solving Eq. (6) using Wit and Bell's estimate of the initial burst, $B_1(f)$.¹ To resolve ambiguity arising from the multiplicity of solutions, $H(f)$ was defined by taking the root with minimum magnitude at each frequency. More formally, $H(f) \equiv H_{\alpha}(f)$, where at each frequency f the root index $\alpha(f)$ was selected from among the four choices $\alpha \in \{1, 2, 3, 4\}$ so that $|H_{\alpha}(f)| = \min_n |H_n(f)|$. This choice generally yields $|H| < 1$, consistent with the physically plausible constraint that the contribution from each subsequent iteration be smaller than the one before it; the resulting geometric series $1 + H + \dots + H^N$ therefore converges as N increases to infinity. We verified the accuracy of the roots by computing the solution residual, defined as $\epsilon = \max_n |q(H_n)|$, and found $\epsilon < 10^{-14}$ at all frequencies.

The solution for the transfer function H is most stable and reliable on the interval 6–8 kHz, where the BM response has the bulk of its energy and the signal-to-noise ratio is therefore favorable. In this region, H generally has the characteristics expected based on the BM response waveform. For example, in the peak region $|H|$ averages about 0.3, consistent with the relative amplitudes of adjacent lobes, and $\angle H$ has a mean slope equivalent to a delay of about 1.1 ms, the approximate time between lobes. These values are

similar to those of analogous parameters obtained by Wit and Bell (2015) using their model. Although visually salient, the sharp spike in $|H|$ evident near 8.3 kHz lies outside the peak region of the BM response and has little functional consequence. The spike arises from the deep notch (or spectral zero) present in the BM response just above CF [see Fig. 1(B)]. Near the BM notch frequency, H becomes exceptionally sensitive to small changes in the ratio D_{BM}/B_1 , and the solution can sometimes produce values $|H|$ close to or exceeding one. Everywhere outside the notch region, the solution to the quartic equation $q(H)=0$ obtained above is well approximated by the expression

$$H \cong 1 - B_1/D_{\text{BM}}, \quad (7)$$

a result obtained by simplifying the quintic equation $qH - q = 0$, assuming that $|H|^5 \ll 1$, and then solving for H . Within the peak region of the BM transfer function, where $|H| \sim 0.3$, the error in this approximation is less than 1%.

The sensitivity of the solution near the BM notch is illustrated in Fig. 3, which demonstrates that H otherwise remains robust to estimates of the initial burst. Wit and Bell (2015) obtain the initial burst by subtracting their model representation of bursts 2–5 from $d_{\text{BM}}(t)$ and then windowing the result to zero after about 1.9 ms. The thin gray lines in Fig. 3 show how $H(f)$ changes when the window cutoff used in this procedure is varied over range of $\pm 10\%$ about this value. Although the changes can be significant near the BM notch, and at other frequencies where the signal-to-noise ratio is relatively poor, changes are small within the peak of the BM transfer function. Subsequent analysis employs a regularized version of H , obtained by applying a low-pass filter with a cutoff at 8.2 kHz (40th-order zero-phase Butterworth), to suppress spurious components at and above the notch frequency.

III. INTERPRETING THE ITERATED PROCESS

Although we have identified an equal, repetitive process capable of producing waxing and waning in the BM response envelope, the mere existence of a solution implies neither that the measured waveform actually arises by this process nor that a physical mechanism with transfer function H resides within the cochlea. To close the loop and understand whether H has any compelling physical meaning, we return to the multiple-internal-reflection model illustrated schematically in Fig. 2.

As emphasized in the diagram, the model has consequences both for BM motion and for ear-canal pressure. To obtain testable predictions, we note that the iterated process involves round-trip wave propagation and reflection, and the transfer function describing the result has the form RR_{stapes} (Shera and Cooper, 2013). In this product, the factor R is the cochlear reflectance, defined as the ratio of the outgoing (i.e., reflected) wave to the ingoing (i.e., stimulus) wave at the base of the cochlea (e.g., Zweig and Shera, 1995; Shera et al., 2005), and the factor R_{stapes} is the reflection coefficient for retrograde waves at the stapes (Shera and Zweig, 1991). One can obtain approximate analytic expressions for the two

FIG. 3. Transfer function of the iterated process. The solid black lines show the (top) magnitude and (bottom) phase of the transfer function $H(f)$ obtained by solving for the roots of Eq. (6). The dashed lines show the spectrum of the initial burst, B_1 , computed as in Wit and Bell (2015). Thin gray lines illustrate variations in H and B_1 induced by modifying the duration of the initial burst in four equal steps spanning the range $\pm 10\%$.

observables shown in Fig. 2—the BM displacement (D_{BM}) and the ear-canal stimulus-frequency otoacoustic emission (SFOAE) pressure (P_{SFOAE})—by solving the equations describing a cochlear model supplemented with mechanical irregularities along the organ of Corti (Shera and Cooper, 2013). Both expressions take the form of power series in RR_{stapes} ,

$$D_{\text{BM}} \cong D_0(1 + RR_{\text{stapes}} + R^2 R_{\text{stapes}}^2 + \cdots), \quad (8)$$

and

$$P_{\text{SFOAE}} \cong P_0(RR_{\text{stapes}} + R^2 R_{\text{stapes}}^2 + \cdots). \quad (9)$$

Although the mathematical formalism of scattering theory was employed in the derivation of these equations (Shera *et al.*, 2005), the expressions are sufficiently general that we expect them to hold independent of the details of emission generation, which are encapsulated in R . Different models of emission generation may yield different expressions for R , but the power-series form of Eqs. (8) and (9) depends only on the iterative nature of the loop. With the identifications $D_0 = B_1$ and $RR_{\text{stapes}} = H$, Eq. (8) for D_{BM} has the same form as Eq. (5), and, to first order, $P_{\text{SFOAE}} \cong P_0 H$.

The multiple-internal-reflection model therefore predicts that the same iterative process responsible for the BM click response also describes the generation of SFOAEs, at least in the low-level linear regime. Because the factor P_0 characterizing round-trip middle-ear transmission varies relatively slowly with frequency compared to RR_{stapes} , the model predicts that the frequency dependence of P_{SFOAE} should be approximately equal to that of the sum $H + H^2 + \cdots$. Figure 4 tests this prediction by comparing the magnitudes and phases of H and $\sum_n H^n$ with measurements of P_{SFOAE} made in the

same animal (Shera and Cooper, 2013). Although cochlear nonlinearities may complicate the comparison, the spectral shapes and phase slopes of these two independent measurements generally match well. The match is especially good in the peak region, where H is well determined.

IV. DISCUSSION

The waxing and waning often seen in BM click responses has been suggested to arise through several non-exclusive mechanisms, including beating between local oscillators and interference effects arising from the internal reflection of cochlear traveling waves (Shera and Cooper, 2013). As shown by Wit and Bell (2015), this latter mechanism, dubbed the multiple-internal-reflection model, predicts the existence of a global, intracochlear feedback loop (see Fig. 2). Working under the assumption of linearity, we show that analysis of the BM click response determines the transfer function, $H(f)$, describing this iterated loop. Our results counter the conclusions of Wit and Bell (2015), who argued, somewhat circularly, that no such H exists and that, consequently, the multiple lobes of the response waveform cannot arise via the “equal, repetitive process” envisioned in the model.

To explore the physical validity of the transfer function H obtained from the data, we test the model prediction that multiple internal reflection produces effects manifest both on the BM (e.g., as a waxing and waning of the click response envelope) and in the ear canal (i.e., as otoacoustic emissions). Comparison with otoacoustic emissions measured in the same animal demonstrates that the same transfer function derived from the BM click response also describes the spectral shape and phase slope of stimulus-frequency OAEs. The transfer function H is thus more than a mere mathematical construct—it has physical consequences consistent with those predicted by the multiple-internal-reflection model. Since purely local models of the BM response waveform yield no natural explanation for the correlated effects measured in ear-canal pressure (Shera and Cooper, 2013), our findings provide compelling support for the multiple-internal-reflection model.

Because Wit and Bell (2015) mistakenly frame their analysis as a critique of the coherent-reflection model of OAE generation, one might misinterpret our contrary results as validating the mechanism of coherent reflection. They do not. Although our results support the multiple-internal-reflection model, they remain logically agnostic to the validity of coherent-reflection theory, whose domain is different. In a nutshell, coherent-reflection theory explains the generation of reverse waves within the cochlea and thus accounts for the empirical form of the cochlear reflectance, R . The concern here, however, is not with understanding how reverse waves come to be, but with the downstream consequences of those waves, and their subsequent reflection from the stapes, both for otoacoustic emissions and for basilar-membrane motion.

A. Accounting for the variety of waveform morphologies

Computation of the individual bursts that sum to form the total waveform provides insight into the emergence of

FIG. 4. Magnitude and phase of P_{SFOAE} (dotted line) compared with those of the transfer function H (dashed line) and the sum $\sum_{n=1}^4 H^n$ (solid line). The SFOAE data, taken from Shera and Cooper (2013), were measured in the same animal responsible for the BM data. As described in the text, the transfer function H was filtered to remove spurious components at the BM notch frequency.

waxing and waning on the BM. Figure 5 illustrates the decomposition of the BM click-response $d_{\text{BM}}(t)$ into successive bursts effected by the transfer function H determined from the data. After the initial burst, subsequent bursts are given by the iteration $b_n(t) = \mathcal{F}^{-1}\{HB_{n-1}\} = h(t) * b_{n-1}(t)$, where $*$ represents a convolution and $\mathcal{F}^{-1}$ is the inverse Fourier transform. The figure demonstrates that, unlike the model bursts employed by Wit and Bell (2015), the bursts $b_{n>1}(t)$ derived here are not just scaled and delayed versions of one another. Rather, because of the filtering that occurs anew with every iteration, higher-order bursts are also increasingly smeared out over time. For example, the second burst begins to rise well before the first burst has subsided.³ Broadening of the temporal envelope of the response is both a general consequence of iterated bandpass filtering⁴ and a natural consequence of dispersive wave propagation and distributed wave scattering in the cochlea. Despite the general broadening of the individual bursts, their phases and other temporal structure have been carefully adjusted, via solution of the equation $q(H) = 0$, so that they sum to yield the more regular and distinct series of lobes seen in the BM waveform. Contrary to the premise underlying the model of Wit and Bell (2015), the iterated process described by the transfer function H yields no direct correspondence between the individual bursts $b_n(t)$ —specifically, their overall shapes and durations—and the lobes of the waveform $d_{\text{BM}}(t)$ they combine to create.

Figure 6 illustrates the sensitivity of the pattern of waxing and waning to the detailed phase relationships among the constituent bursts. The figure shows both the original BM click response and a simulated waveform synthesized from the initial burst after modifying the transfer function H to include an additional delay (thus, $\hat{H} = He^{-i\omega\tau}$, with $\tau = 50 \mu\text{s}$). Modifications like this are just a convenient way to simulate the possible results of measuring BM motion at different locations within the cochlea. Other measurement locations will generally exhibit different characteristic frequencies (CFs) and near-CF group delays (but see Shera, 2015), and wave scattering at corresponding frequencies will

FIG. 5. Individual bursts produced by iterating the regularized transfer function H . The five bursts (black lines, labeled on the left) sum to yield the total waveform (gray line, partially concealed by the first burst).

FIG. 6. Simulated click response at another measurement location. The bottom panel shows the waveform synthesized using the initial burst and the transfer function $\hat{H}$, obtained from H by incorporating an additional $50 \mu\text{s}$ delay. For comparison, the top panel shows the original, measured click response, reproduced from Fig. 1.

typically engage different arrays of micromechanical irregularities or other emission generators. All these changes modify the phase of the cochlear reflectance, R , and thus of H .

The bottom panel of Fig. 6 shows that despite involving a minor change to the transfer function, the waveform reconstructed from $\hat{H}$ manifests a strikingly different temporal structure. Although the click response remains prolonged in time, distinct lobes are no longer apparent in the envelope. Constituent bursts whose relative phases previously produced periodic cancellations in the waveform now add constructively and blend smoothly together. Although the BM click response illustrated in Fig. 1 was recorded at a measurement location and click level where the lobes appear especially regular and distinct, heterogeneity in the shape of the envelope, evident here in the model, is also a general feature of click responses measured *in vivo* (Recio *et al.*, 1998; Lin and Guinan, 2000; Rhode, 2007; Guinan and Cooper, 2008). Thus, a single iterated process of multiple internal reflection can generate the variety of response envelopes observed experimentally, including cases where the iterative nature of the process seems almost too obvious and others where it appears almost fully obscured.

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³For aesthetic reasons, we followed Wit and Bell (2015) by cleansing and gently massaging the measured click response prior to analysis. As they did, we removed high-frequency noise from the waveform using a 20th-order, zero-phase Butterworth filter with a cutoff frequency of 10 kHz. In addition, after tapering the waveform to zero at the end (using a 20th-order Butterworth window with a cutoff time of 5.7 ms), we improved the frequency resolution of the Fourier analysis by extending the 6-ms waveform to 10.2 ms (2048 points) by zero-padding. This last operation assumes, in effect, that had the BM measurement time been extended further, any additional lobes that might have been present in the measured click response after 6 ms would be small enough to be neglected. None of the operations described in this footnote have any qualitative effect on our conclusions.

²In the notation of Shera and Cooper (2013), the functions D_0 and P_{SFOAE} have the values $D_0 = P_S G_{\text{ME}}^{-1} W_r Y_{\text{BM}} / i\omega$ and $P_0 = P_S G_{\text{ME}}^{-1} (1 + R_{\text{stapes}}) / R_{\text{stapes}}$.

³Close examination of bursts 2–5 in Fig. 5 reveals miniature ongoing oscillations present both before and after the main lobe of each burst. Precursor and postcursor oscillations with an amplitude close to the noise floor (i.e., smaller than the highest-order burst visible in the data) arise as artifacts of the Fourier-based solution method, which effectively assumes that each individual burst is periodic (with period 10.2 ms; see footnote 1), together with the constraint that bursts 2–5 sum to zero at early and late times.

⁴In their Fig. 7, Wit and Bell (2015) illustrate this broadening—and implicitly contrast it with behavior of the all-pass filters assumed in their model—using a series of three identical Gaussian bandpass filters.

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