Mistakes and Misrepresentations in Heil, Neubauer, and Irvine (2011): Why Their Improved Equation is Not, and the Root Cause of Their Failure, and How the Nizami-Schneider Equation Already Deals with that Root Cause

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***Abstract*—Many investigators have assumed that some physical and physiological mechanisms of hearing can be elucidated by crafting equations for the voltage-spike-firing rate of an auditory-nerve fiber as a function of the root-mean-square (RMS) intensity of an applied single-frequency tone. In this vein, Heil, Neubauer, and Irvine proposed an "improved" variation of the well-advertized saturating power function of Sachs and Abbas. Here it is shown, however, that Heil et al. committed a number of egregious errors that render their contribution spurious, and in so doing, they misrepresented an existing equation, the Nizami-Schneider equation, which does many of the things that other equations (including those of Heil et al.) do not. Heil et al. failed because of an unrecognized problem that continues to elude mention in the literature, namely, that there are contradictory limits for the stimulus intensity which is called "threshold". Effectively, Heil et al. assumed that threshold is infinitely low in decibels, a notion widely attributed to Swets. But a closer look at Swets' paper reveals no compelling evidence for infinitely low thresholds. In contrast to Heil et al., the Nizami-Schneider equation avoids an infinitely low threshold, because their threshold corresponds to some firing rate just in excess of the spontaneous firing rate. This interpretation of threshold jibes with recent realizations that loudness, a sensation caused by auditory-nerve-fiber firing, must be nonzero at the psychological tone-detection threshold. Finally, for some fibers, the slope of the plot of firing rate versus intensity suddenly decreases in the middle of the fiber's range of firing, and remains lower until firing rate eventually saturates. Any truly "improved" rate-level function might attempt to describe this so-called "sloping-saturation", but Heil et al. ignored it. Sloping-saturation is, in fact, well-fitted by an extended version of the Nizami-Schneider equation.**

***Index Terms*—auditory, equation, firing, loudness, spikes**

I. INTRODUCTION

OVER the preceding five decades, it has been thought useful to devise equations, having regression-fitted parameters, to describe the voltage-spike-firing rate of auditory primary afferent neurons as a function of the root-mean-square (RMS) level of the applied pure-tone (i.e., single-frequency) stimulus. It was thought that a well-fitting rate-level equation would aid in the comprehension of the underlying physical and physiological mechanisms of hearing. The plot of firing rate versus stimulus intensity (the "rate-level plot") of the neuron, given a stimulus at the neuron's CF (characteristic frequency, that pure-tone frequency at which it responds most strongly), has four salient properties: spontaneous firing rate (in spikes/s), threshold intensity for firing above spontaneous rate (in dB SPL), saturation (i.e., maximum observed) firing rate, and dynamic range (colloquially, the width of the rising portion of the plot, in decibels). How well any proposed rate-level equation accounts for these properties may be defined qualitatively as that equation's efficacy. Various rate-level equations have been published, but none has proven ideal (as discussed in [1]-[3]).

Hence, any claim of improvement is worthy of scrutiny. Heil, Neubauer, and Irvine [4], in "An improved model for the rate–level functions of auditory-nerve fibers", proposed a saturating power function to describe pure-tone-driven empirical rate-level plots for primary auditory afferents of the cat. Their equation is a variation on one published by Sachs and Abbas [5] for the same purpose, but which, contrary to some implications in Heil et al. [4] and in Sachs and Abbas [5], was not the first of its kind (Appendix). Regardless, Heil et al. ([4], p. 15424) perceived a flaw in the Sachs-Abbas equation: "This model … does not predict the correlation of spontaneous [neuronal firing] rate with ANF [auditory-nerve fiber] sensitivity observed in mammals and cannot account for spike rates lower than the spontaneous rate" (terms in square brackets are supplied). Heil et al. [4] perceived other flaws, but their attempts to correct the flaw that is mentioned in the quotation forms the core of Heil et al. [4]. By "sensitivity", Heil et al. [4] effectively meant the stimulus intensity at which the fiber fires just above its spontaneous firing rate, the stimulus intensity commonly known as the fiber's "threshold". It takes some reading to discern this, however, as the concept of "sensitivity" has been used by them and others to refer to the intensity that corresponds to some other point on a rate-level plot, such as its midpoint.

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II. The Heil, Neubauer, and Irvine [4] saturating power function, Part 1: "RA" (Rate-Additivity)

A. The Heil et al. [4] "RA" (Rate-Additivity) Equation

Heil et al. ([4], p. 15426) first note that "At frequencies around the fiber's CF, BM [basilar membrane] displacement grows in a nonlinear ("compressive") manner with stimulus amplitude" (terms in square brackets are supplied). Hence, Heil et al. (p. 15426) chose to "consider only responses to frequencies well below the CF, where BM displacement can be well approximated as a linear function of stimulus amplitude P (in pascals)". Note well that "stimulus amplitude" must, as in all relevant papers, refer to RMS (root-mean-square) amplitude of the pressure wave, not its instantaneous amplitude above or below ambient air pressure.

Most of the relevant published literature concerns tones at CF (reviewed in [1], [6], [7]). Heil et al.'s [4] focus would therefore seem too off-CF to render their work very useful. As Heil et al. ([4], p. 15426) themselves noted, the Sachs and Abbas [5] equation itself was not restricted to off-CF frequencies. But for Heil et al. [4] such restriction "reduces the number of [our] model parameters from six to four" ([4], p. 15426; terms in square brackets are supplied), although why six parameters would have been needed in the first place was not explained. In Section 5 of the present paper, a likely explanation will be supplied. Heil et al. [4] would have been well-justified in noting the Nizami and Schneider [1] equation, which has a version that can describe nonlinearity at CF using six parameters reduced to five (e.g., [1], [3], [8]). More on this in Section V.

Heil et al. ([4], p. 15426) next introduced the parameters of their equation. R_{spont} denoted the spontaneous voltage-spike-firing rate of the fiber; $R_{\text{max d}}$ denoted the maximum "driven rate", that is, the maximum firing-rate that the fiber is capable of, minus it's spontaneous rate. Heil et al. ([4], p. 15426) then rewrote the principal equation of Sachs and Abbas [5], as follows:

$$R(P) = \frac{R_{\text{max d}} \cdot P^{\alpha}}{K_{\text{RA}}^{-1} + P^{\alpha}} + R_{\text{spont}}, \quad \alpha > 0, \qquad (1)$$

where "The parameter K_{RA} is a measure of sensitivity (in units of pascals (Pa) raised to the power of – *α*, $\text{Pa}^{-\alpha}$)" ([4], p. 15426). In Sachs and Abbas [5], P refers to RMS stimulus pressure.

B. The Shortcomings of the Heil et al. [4] "RA" Equation, According to Heil et al. Themselves

Remarkably, having introduced this model, Heil et al. [4] then abandoned it. Their primary reason was evidently that "it provides no explanation of differences in spontaneous activity or of why ANFs should be spontaneously active at all" ([4], p. 15427). Heil et al. did not explain why their model should have properties whose origins would seem to depend upon profound issues of biophysics, which require profound skills to understand. Regardless, Heil et al. (p. 15427) made a further complaint, regarding an issue implied to be related (although they did not explain how): "The model also provides no explanation of the tight positive correlation in mammals between spontaneous rate and what we will term 'intrinsic sensitivity'". By 'intrinsic sensitivity', as Heil et al. explained (but in a somewhat convoluted fashion), they apparently meant threshold of response of a fiber to a tone of a given frequency. Threshold is well-known to vary across fibers at a given CF (reviewed in [1]; citations too numerous to mention). Heil et al. ([4], p. 15427) further declared that "A tight positive correlation between spontaneous rate and intrinsic sensitivity, however, is universally observed in mammalian ANFs". They cited, as support, four papers that altogether represent two laboratories.

There are, however, far more than four papers published on the matter, representing many more than two laboratories. And indeed, whether there is any correlation at all between spontaneous rate and 'intrinsic sensitivity' in any mammalian species seems to be a matter of opinion, at best. Nizami and Schneider [1] – a paper cited by Heil et al. [4] – noted a lack of correlation between spontaneous rate and 'intrinsic sensitivity', and cited four supporting papers [9]-[12], altogether representing three laboratories. Since that time, no convincing evidence of correlation has emerged.

This point will prove important, and will be returned to later. Meanwhile, let us attend to another important point. That is, Heil et al. ([4], p. 15427) declared that there was yet another limitation of Eq. (1), namely, that "it cannot account for spike rates lower than the spontaneous rate". And, indeed, a drop to below-spontaneous firing rates has sometimes been observed immediately post-stimulus. (This phenomenon is not in question, hence the numerous supporting citations are presently omitted.) But the Heil et al. approach to quantifying the phenomenon proves to be extraordinary, as will be described.

C. The Values (Allegedly Derived from Nizami [6]) of the Parameter α in the Heil et al. [4] "RA" equation: Part 1

First, however, yet another problem that Heil et al. ([4], p. 15427) noted about Eq. (1) must be mentioned: "the lack of any physiological explanation" of published values of the parameter α. The latter are quite variable (cited in [4]). Heil et al. [4] had nonetheless calculated α "from the parameters listed in his paper" ([4], p. 15428), "his" referring here to Nizami [6].

The calculations of Heil et al. [4] are unusual and deserve scrutiny. To do so, some backtracking is needed. Heil et al. ([4], p. 15426) had noted that Sachs and Abbas [5] had presented a normalized version of their equation, which in Heil et al.'s [4] notation is

$$\frac{R(P) - R_{\text{spont}}}{R_{\text{max d}}} = \frac{P^{\alpha}}{K_{\text{RA}}^{-1} + P^{\alpha}} = \frac{1}{1 + K_{\text{RA}}^{-1} \cdot P^{-\alpha}}. \qquad (2)$$

Heil et al. then noted that this equation is a *logistic*, and that "Nizami and Schneider (1997) and Nizami (2002) proposed the logistic equation, with threshold (in decibels SPL) and dynamic range (DR; in decibels) as explicit parameters

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instead of K_{RA} and *α*, without acknowledging its equivalence to the saturating power function proposed by Sachs and Abbas (1974)" ([4], p. 15427). This quotation implies a lack of collegiality by Nizami and by Schneider, and it deserves a response. And indeed, Nizami and Schneider [1] and Nizami [6], *as well as a variety of other sources* co-authored by Nizami ([2], [3], [13]-[16]), did *not* declare equivalence of the Nizami–Schneider rate-level equation to the saturating power function of Sachs and Abbas [5], because the two equations are *not* in fact equivalent, as follows.

D. A Proven Alternative to the Heil et al. [4] "RA" Equation and Other Saturating Power Functions: the Nizami-Schneider Rate-Level Equation

In keeping with the Nizami and Schneider [1] notation, let us use *r* in place of *R*. The Nizami–Schneider equation is

$$r(x)=\frac{r_{\max}-r_s}{1+\left(\dfrac{100-c}{c}\right)^{\left[1-2\cdot\left(\frac{x-\varepsilon}{\lambda}\right)\right]}}+r_s, \qquad -\infty\le x\le\infty. \tag{3}$$

Here *x* is RMS (root-mean-square) intensity, expressed in dB SPL, of the single-frequency ("pure-tone") stimulus. *c* is a unitless dynamic-range-associated parameter, to be set by the user. There were four parameters to be obtained by fitting Eq. (3) to rate-level plots: $r_{\max}$, r_s, ε, and λ. $r_{\max}$ is saturation firing rate (i.e., the maximum that the neuron can produce) in spikes/s; r_s is spontaneous firing rate; ε is threshold, in dB SPL, for firing above spontaneous rate; and λ is dynamic range, in decibels. The fit of Eq. (3) does not depend upon *c*, which can assume any value between 0 and 50 during fitting to data; to achieve a sensible fitted value for λ, the user must choose a sensible value for *c*. *c* = 2 proves to be appropriate [6]. Note that $r(x)\rightarrow r_s$ as $x\rightarrow-\infty$ dB SPL and that $r(x)\rightarrow r_{\max}$ as $x\rightarrow\infty$ dB SPL. That is, the spontaneous and saturation rates are approached infinitely slowly.

Infinitely low limits for the stimulus-evoked firing of auditory-nerve fibers is unrealistic (this point is explained in Section IV.B. below). In this respect, the Nizami-Schneider formulation is actually advantageous, as follows. At fiber threshold ε it allows a firing rate in excess of r_s. Now, the experience of *loudness* has always been presumed to arise from above-spontaneous-rate firing in auditory-nerve fibers (no citations required). Hence, if the auditory-nerve-fiber threshold is the origin of the threshold for loudness – a reasonable assumption – then loudness at its "threshold" should be non-zero, a result arising from experiment as well as theory (e.g., [17]-[20]).

Following Nizami ([6], p. 19), we can define terms $\zeta=\lambda/\left[2\ln\left((100-c)/c\right)\right]$ and $\eta=\varepsilon+(\lambda/2)$, so that from Eq. (3),

$$r(x)=\frac{r_{\max}-r_s}{1+e^{-\left(\frac{x-\eta}{\zeta}\right)}}+r_s. \tag{4}$$

Nizami and Schneider [1] and Nizami [6] showed that when Eq (4) was fitted to any sigmoid-shaped empirical plot of firing rate versus stimulus intensity, the parameters ζ and η proved to have the same values across curve-fits when those fits commenced using different starting values of the parameters (non-sigmoidal data-plots will be dealt with shortly). This is a highly desirable outcome, referred to by engineers, for whom consistent values are crucial, as "robustness".

Equation (3) was derived from first principles. Its purpose was to do something that had evidently not yet been attempted by Sachs and Abbas [5] or by anyone else working in auditory neuroscience, namely, to bring dynamic range into a rate-level equation as a parameter ([1], [2], [6], [13], [14]). In contrast, saturating power functions inherently imply a fixed dynamic range, when the latter is inferred according to mathematical rules set in the literature, those that relate to the fit of rate-level equations (see Nizami 2002, p. 23 and Appendix). This insight was separately and simultaneously made by L. Nizami and by B. A. Schneider. Their conclusion has never been disputed. Remarkably, Heil et al. ([4], p. 15432) acknowledged their insight: "According to the RA model, and in the absence of BM nonlinearities, the DRs of all rate-level functions would be identical if the exponent α were fixed [a point made by Nizami (2002)]". But Heil et al. [4] failed to clarify a related important point, namely, that the old procedures used by Sachs and Abbas [5] and by others for estimating the dynamic range of a neuron are still employed. The insight of Nizami and of Schneider formed the impetus for Eq. (3), which was introduced in Nizami and Schneider [15] and later thoroughly explained and explored ([1]-[3], [6]-[8], [13], [14], [16], [21]-[23]).

E. The Nizami-Schneider Equation Versus That of Sachs and Abbas [5]

Recall again Heil et al.'s statement ([4], p. 15427) that "Nizami and Schneider (1997) and Nizami (2002) proposed the logistic equation, with threshold (in decibels SPL) and dynamic range (DR; in decibels) as explicit parameters instead of K_{RA} and α, without acknowledging its equivalence to the saturating power function proposed by Sachs and Abbas (1974)". Emphatically, the Nizami-Schneider derivation was *not* modeled on a Sachs and Abbas [5] derivation of a saturating power function, because Sachs and Abbas [5] did not provide such a derivation per se. Indeed, the Sachs-Abbas equation bears a striking resemblance to an earlier equation for auditory response, that of Adams [24] (see the present Appendix). All told, any credit to Sachs and Abbas [5] by Nizami and by Schneider would have been inappropriate and misleading.

In sum, Nizami and Schneider [1] and Nizami [6] had not, as Heil et al. ([4], p. 15427) implied, unfairly ignored the work of Sachs and Abbas [5]. On the contrary, Nizami and

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Schneider [1] and Nizami [6] had given it such rigorous scrutiny that they had found a significant hidden drawback to it, one that Heil et al. ([4], p. 15432) had credited to Nizami [6]. Note that Eq. (4) can be rewritten as

$$\frac{r(x)-r_s}{r_{\max}-r_s}=\frac{1}{1+e^{-\left(\frac{x-\eta}{\zeta}\right)}}. \quad (5)$$

Equation (5) is *not*, contrary to Heil et al. [4], equivalent to Eq. (2). A lack of equivalence is evident from term-by-term comparison. The parameters of Eqs. (2) and (5) have different meanings.

F. The Values (Allegedly Derived from Nizami [6]) of the Parameter α in the Heil et al. [4] "RA" Equation: Part 2

The reader is now hopefully sufficiently informed to return to Heil et al.'s [4] claim to have calculated α "from the parameters listed in his [i.e., Nizami's] paper" ([4], p. 15428). Remarkably, Heil et al. did not show *how* they did this. Personal communications to Professor Peter Heil did not clarify the matter. What relations did Heil et al. [4] actually use to infer α from K_{RA} and η and ζ? No answer is apparent; Heil et al. [4] also failed to explain from what part of Nizami [6] they had inferred the necessary values of η and ζ. In fact, the latter two alone can be respectively derived from the values of ε and λ found in Table 2 of Nizami [6].

Using data from Nizami [6], Heil et al. ([4], p. 15428) allegedly found "a negative correlation between α and the logarithm of spontaneous rate". But their data source from Nizami [6] could only have been Nizami's Table 2, which was meant only to show a limited number of examples of the fitted parameter values of Eq. (3). Hence Nizami's Table 2 contained just fifteen entries of each of ε and λ (of which 7 were obtained by fitting rate-level plots from Sachs' own laboratory) for any given value of the user-chosen Nizami-Schneider parameter *c* (see above). Now, fifteen entries hardly seems sufficient to find any convincing relation of α to [the logarithm of] spontaneous rate, and the magnitude of Heil et al.'s [4] relevant correlation coefficient r^2, 0.19, is too small to suggest any real "correlation".

Aside from speculation about how Heil et al. [4] had actually processed the Nizami [6] data, the poor correlation declared by Heil et al. [4] is important in its own right, because Heil et al. ([4], p. 15427) used it as partial justification for abandoning their "RA" model (Eq. (1)) and replacing it with their "AA" model, to now be described. The description of the "AA" model will reveal fatal flaws that render the Heil et al. [4] approach unusable overall.

III. The Heil et al. [4] Saturating Power Function, Part 2: "AA" (Amplitude-Additivity), and Some Hidden Problems with It

A. The Heil et al. [4] "AA" Equation: Heil et al. Invoke the "Physiological Stimulus"

Heil et al. ([4], p. 15428) then proceeded to take a different tack. Their change of approach is best expressed in their own words: "We assume that R_{spont} is produced by a physiological stimulus that is present at rest and that is identical in nature to that produced by the sound". Their next line stated that "The stimulus at rest, like the sound stimulus, can therefore be expressed in terms of amplitude". A "physiological stimulus", Heil et al.'s "The stimulus at rest", is presumably something within the body that is equivalent to an external stimulus. Heil et al. proposed to assign to the "physiological stimulus" an actual stimulus intensity, presumably so as to avoid mixing internal units (those of the "physiological stimulus") and external units (those of the actual external stimulus, what Heil et al. called the "sound"). At first glance, Heil et al.'s new approach seems like gibberish. On second reading, it has a familiar ring to it. This particular gambit dates at least as far back as Zwislocki [25], whose work was later emulated concept-by-concept (and hence equation-by-equation) by Moore, Glasberg, and Baer [26], whose equations were incorporated into a new ANSI Loudness Standard [27]. But Heil et al. [4] cite neither Zwislocki [25] nor Moore et al. [26] nor the ANSI Loudness Standard.

Heil et al. ([4], p. 15428) refer to "the amplitude of the resting stimulus" as P_0, "which sets the point of operation and to which the effects of the sound amplitude add" ([4], p. 15428). Hence the name "Amplitude-Additivity" for their model. But "sets the point of operation" seems unclear. Regardless, the Amplitude-Additivity equation ([4], p. 15428) was then

$$R(P)=\frac{R_{\max}\cdot(P+P_0)^{\beta}}{K_{\mathrm{AA}}^{-1}+(P+P_0)^{\beta}}, \quad P\ge -P_0,\ \ \beta>0, \quad (6a)$$

$$R(P)=0, \quad P<-P_0. \quad (6b)$$

Heil et al.'s $R_{\max}$ denoted the maximum spike-firing-rate achievable by the fiber (called $r_{\max}$ by Nizami and Schneider [1]; see Eq. (3) above). The symbol β replaced α, and the term K_{AA} replaced K_{RA}. Note well the absence of the spontaneous firing rate R_{spont}. Note also that the limit $\{-P_0\}$ will be a negative number, because P_0 itself was clearly meant to be a positive number. The stimulus amplitude *P* is always defined in the literature as a root-mean-square (RMS) – that is, as a *positive* – quantity. Hence, Eq. (6a) allows voltage spikes for a subzero stimulus intensity, which is an impossibility when stimulus intensity is RMS as usual. But a negative pressure does not account for the spontaneous firing of the fiber and, more to the point, is unphysical. A negative *P* is not a feature of the Nizami-Schneider equation (Eq. (3)).

B. The Heil et al. [4] "AA" Equation: Heil et al. Re-introduce the Spontaneous Firing Rate

To continue: Heil et al. ([4], p. 15428) then re-introduced

R_{spont}, by *stipulating* that $R(0) = R_{\text{spont}}$. For Heil et al. [4], from Eq. (6a) above,

$$R(0) = R_{\text{spont}} = \frac{R_{\text{max}} \cdot P_0^{\beta}}{K_{\text{AA}}^{-1} + P_0^{\beta}}. \tag{7}$$

Now Heil et al. introduced *S*, defined as

$$S = K_{AA} \cdot P_0^{\beta} = \frac{R_{\text{spont}}}{R_{\text{max}} - R_{\text{spont}}}. \tag{8}$$

Heil et al. ([4], p. 15428) then rewrote their Amplitude-Additivity rate-level equation (Eq. (6a) above) as

$$R(P) = \frac{R_{\text{max}}}{1 + S^{-1} \cdot (1 + P/P_0)^{-\beta}}. \tag{9}$$

Bearing in mind that $\beta > 0$, then for compliance with Eqs. (6a) and (6b), $R(-P_0) = 0$.

C. *The Heil et al. (2011) "AA" Equation: "Emergent" Properties*

Heil et al. (2011, p. 15429) next declared that "Spontaneous activity and its hitherto unexplained tight correlation with the intrinsic sensitivity of ANFs are emergent properties of the AA model". They qualified this alleged "tight correlation" – which, as noted above, was questionable – by arguing that from Eqs. (7)-(9), if $R_{\text{max}} >> R_{\text{spont}}$ then $R_{\text{spont}} \cong R_{\text{max}} \cdot S$. Heil et al. ([4], p. 15429) then declared that "R_{spont} will vary in nearly direct proportion to the fibers' intrinsic sensitivity, *S*". They failed to note an important point – namely, that most auditory-nerve primary afferents in mammals do *not* in fact obey $R_{\text{max}} >> R_{\text{spont}}$ (reviewed in [1], [6], [7]). Also, what Heil et al. [4] call a "tight correlation" is not an *emergent* property of the AA model; on the contrary, Heil et al. had engineered it in all along, by *stipulating* that $R(0) = R_{\text{spont}}$, which is hardly "emergent" from Eqs. (6a) and (6b).

Heil et al. ([4], p. 15429) also claimed that "The AA model can also readily account for spike rates lower than R_{spont}". That is, "It merely requires *P* to be negative" ([4], p. 15429). But a negative pressure is a key assumption of the Heil et al. approach, and, as noted above, the very idea of a negative *P* is absurd. Heil et al. continued: "On this view, P_0 defines the point of operation about which $R(P)$ can be modulated up to R_{max} or down to 0 by positive and negative amplitudes, respectively (e.g., by positive and negative instantaneous pressures at low frequencies" ([4], p. 15429). This statement represents an even tighter restriction than before; the Heil et al. rate-level equation (Eq. (6a)), at first only applicable to pure tones of frequencies well-below CF, is now effectively restricted to *low CFs* as well, although we are not told how low. The answers may lie in Heil et al.'s [4] new implication, namely, that their stimulus-amplitude variable, P, refers to "positive and negative instantaneous pressures", rather than to the stimulus-amplitude measure used by their claimed progenitors, Sachs and Abbas [5], namely, RMS pressure.

Heil et al. ([4], p. 15429, and onwards) devoted eight further printed pages to attempting to justify various values for the parameters of their equation, through a variety of allusions to the literature, as well as through various curve-fitting exercises. However, in view of the flaws revealed above, such efforts seem spurious.

IV. Why do the Heil et al. [4] Equations Fail? The Root Causes are in the Limits that Such Equations are Required to Account For

A. *Contradictory Stimulus-Intensity Limits for "Threshold"*

It is time to introduce a crucial point that is not discussed in the literature on hearing, but for which discussion is well-overdue. First note that the literature contains no agreement on how to discern the intensity at which an auditory primary afferent fiber reaches its threshold for stimulus-evoked firing. Rather, threshold criteria are used, which represent opinions rather than certainties (reviewed in [1], [3], [6], [7]). The reasons for the uncertainties, now to be discussed, represent fundamental problems for the crafting of rate-level equations.

Let us imagine RMS stimulus amplitudes P, and the resulting evoked firing rates, as both decrease. Then $R(P) \to R_{\text{spont}}$ as $P \to 0$. However, if we stipulate P_{th} to be "threshold" amplitude, then $R(P) \to R_{\text{spont}}$ as $P \to P_{\text{th}}$. Thus, there are contradictory amplitude limits for "threshold", which are independent of the actual value of R_{spont}. Those limits cannot be dealt with by assuming that $P_{\text{th}} = 0$, because a pressure amplitude of 0 corresponds to $-\infty$ dB SPL, the unreachable low-intensity extent of the decibel scale. Such an infinitely low threshold defies the very concept of threshold as something finite. (A decibel scale is used because just-noticeable-differences in intensity are closer to constant on such a logarithmic scale ("Weber's Law") than on a linear scale.) As Wever and Zener had noted many years earlier ([28], p. 491), "we could not take seriously a measure of sensitivity at infinity". *Prima facie* it seems ludicrous to believe that a stimulus of, say, - 200 dB SPL could ever be "detected", even if ongoing.

Heil et al. [4] showed no inkling of the problem of contradictory intensity limits as firing rate approaches the spontaneous rate. Heil et al. [4] assumed that $R(P) \to R_{\text{spont}}$ as $P \to 0$, i.e., they effectively assumed that $P_{\text{th}} = 0$ under the intuitive notion that threshold is the stimulus value at which spike-firing-rate just exceeds the spontaneous firing rate. But Heil et al. [4] also allowed lower-than-spontaneous firing rates for negative values of P. When P has its normal interpretation as RMS stimulus

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amplitudes, the notion of negative values of P is ludicrous. Nizami and Schneider [1] and Nizami [6] avoided this illogicality by assuming that $r(x) \to r_s$ as $x \to -\infty$ dB SPL. At first, this appears to confirm an infinitely low fiber threshold, but note well that Nizami and Schneider avoided $P_{\text{th}} = 0$ by engineering their threshold ε to occur at a firing rate just in excess of r_s, in agreement with the notion that loudness is non-zero at stimulus-detection threshold (see Section II.D., above).

B. Is Threshold Infinitely Low?

The notion of threshold at $-\infty$ dB SPL has been accepted by many. Therefore, before proceeding further, let us briefly examine its origins. It is widely attributed to Swets [29]. Swets' arguments concerned a model of psychophysical behavior called Signal Detection Theory (here, denoted SDT), to which he contributed (e.g., [30]). Swets [29] produced a review of SDT as it was laid out at the time, including a key SDT concept, that of the "ideal observer". Swets noted that in a typical psychophysical detection task, the listener decides whether a *Signal* is present, or only a background *Noise*, based (hypothetically, according to SDT) upon the logarithm of the ratio of the likelihood of *Signal+Noise* to the likelihood of Noise alone. That log-likelihood ratio obeys two distributions – one for Signal+Noise and one for Noise – and the listener places a hypothetical decision-making criterion somewhere along that log-likelihood-ratio continuum. Because those distributions have infinitely long tails, an infinitely-low-decibel threshold is (hypothetically) possible.

Swets [29] proceeded by reviewing the successful application of SDT to data from Yes/No, second-choice, and rating experiments, in the context of what that success meant for five threshold models (which were not SDT models) "concerning the processes underlying these data" ([29], p. 175). Swets' analysis was long and complicated, and it defies synopsis. But his conclusions were hardly firm; in fact, Swets was oddly equivocal. First, he noted that one of the models that he examined fit none of the data; then, that two of the models fit some of the data; then, that another of the models could not be evaluated at all using the data; and finally, that one of the models fit *all* of the data, as too did SDT. Swets ([29], p. 176) concluded that "The outcome is that, as far as we know, there *may* be a sensory threshold" (italics added). He started his next paragraph with "On the other hand, the existence of a sensory threshold has not been demonstrated". The latter turnabout seems especially odd, in light of some shortcomings of SDT which Swets ([29], p. 172) noted, namely, that "the human observer, of course, performs less well than does the ideal observer in the great majority of detection tasks, if not in all". That finding has been replicated many times over (see [30]; for intensity discriminability, for example, see [1], [7], [23]). In sum, Swets [29] did not produce compelling evidence of an infinitely low threshold.

The same year that Swets implied an infinitely low threshold, Hellman and Zwislocki ([31], p. 687) stated the contrary view that "The threshold of audibility is a natural boundary condition which cannot be eliminated". There is no reason to debate that view.

V. Sloping-Saturation: A Phenomenon Considered Important, but Ignored by Heil et al. [4]

A. Sloping-Saturation of the Firing Rates of Auditory-Nerve Fibers

Recall from above that Heil et al. [4] restricted their equation to single-frequency ("pure") tones whose effects are far from the BM locus for which the pure-tone-evoked firing has its lowest thresholds (i.e., the position of the CF). Their reasoning was that, off-CF, "BM displacement can be well approximated as a linear function of stimulus amplitude P" ([4], p. 15426). Their statement implies that nonlinear BM displacement at CF results in rate-level plots that are not sigmoidal when rate is plotted versus amplitude using a logarithmic scale for amplitude (for example, dB SPL). That is, Heil et al. [4] implied that rate-level plots are "sloping-saturating", that is, having a sharp bend in its middle followed (with further increase in stimulus amplitude) by an upper, lesser slope (see for example [5]; [32], Fig. 1; also [1], [6], [7]). However, as Nizami and Schneider [1] and Nizami [6] had noted in passing, most rate-level plots are sigmoidal even at the CF place on the BM. Notwithstanding, many authors alleged (and none proved) a relation between sloping-saturation and the intensity-dependence of the BM displacement. Such a relation may reflect only wishful thinking, as Nizami [7] noted based on strong empirical evidence (see [11], [32], [33]).

Regardless of the origin of sloping-saturating firing, there are "ideal-observer" computations ([1], [7]) taken after Signal Detection Theory [30] which suggest that sloping-saturating firing does not add appreciably to the encoding of stimulus intensity. The requisite analysis first required that sloping-saturating firing-rate plots be fitted well to an equation (one soon to be described). In contrast, Heil et al. [4], as noted above, had avoided "the complications of BM nonlinearities" ([4], p. 15426). Their reluctance is remarkable, especially considering that the equation which they chose to "improve" upon, that of Sachs and Abbas [5], contained within itself an equation for nonlinear BM displacement ([5], p. 1840; see the present Appendix). Heil et al. [4] ignored the displacement equation offered by Sachs and Abbas [5]. Instead, Heil et al. [4] chose to phrase the Sachs-Abbas firing-rate equation in a generalized form as a function of the amplitude of the pure-tone stimulus (e.g., Eq. (1) above).

Sachs, Winslow, and Sokolowski [34] had already attempted one of Heil et al.'s [4] stated goals, namely, of improving upon the Sachs and Abbas [5] equation. Therefore, we might expect Heil et al. [4] to have discussed the changes that Sachs et al. [34] had effected. Remarkably, however, Heil et al. [4] largely ignored Sachs et al. [34], save to casually cite them in passing ([4], p. 15427).

B. The "Sloping-Saturating" Equation of Sachs et al. [34]

It proves worthwhile to explore what Sachs et al. [34] did. They introduced their efforts by stating, with respect to Sachs and Abbas [5], that "Although that model was able to

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provide qualitatively good fits to the auditory nerve data, its dependence on the basilar-membrane data limited its computational usefulness” ([34], p. 61). Of course, the Sachs and Abbas [5] equation did not, in fact, “provide qualitatively good fits to the auditory nerve data”. Rather, “Such equations, when fitted, show systematic deviations of the smooth curve from the data, deviations that can be discerned with the naked eye” ([6], p. 23). Nizami [6] explained that such deviations are due to the fixed dynamic range that ensues when the exponent α is held constant (as noted well-above).

Sachs et al. ([34], p. 64) used an exponent that they called *α*, which they held constant. Sachs et al. ([34], p. 62) nonetheless described their new model as “a computationally tractable form of the original Sachs-Abbas model”. Their new equation was (in their own notation)

$$\mathrm{R_{TOT}} = \frac{\mathrm{R_M}\left[\widehat{\mathrm{P}}/\theta_{\mathrm{E}}\right]^{1.77}}{1+\left[\widehat{\mathrm{P}}/\theta_{\mathrm{E}}\right]^{1.77}} + \mathrm{R_{SP}}. \tag{10a}$$

$\mathrm{R_M}$ is the equivalent of $r_{\max} - r_s$ in Eq (3) above; θ_{E} “effectively determines the excitatory threshold of the model” ([34], p. 64); and $\mathrm{R_{SP}}$ is the spontaneous firing rate. $\widehat{\mathrm{P}}$ is the stimulus-amplitude, defined as

$$\widehat{\mathrm{P}} = \mathrm{P}\cdot\left(\frac{1}{1+\left(\mathrm{P}/\theta_{\mathrm{I}}\right)^2}\right)^{\alpha}, \tag{10b}$$

where θ_{I} was called the “compression threshold”, the stimulus intensity at which the bend in sloping-saturation occurs ([34], p. 64). Sachs et al. ([34], p. 65) set $\alpha = 1/3$, after the same displacement data that they had used in Sachs and Abbas [5] to set the power exponent there (see the present Appendix). As such, Eq. (10a) has four parameters to be obtained through fitting to rate-level plots. Those parameters are not independent; as Nizami [6] had noted, θ_{E} inversely correlates to both the lower slope and the upper slope of sloping-saturating rate-level plots. Altogether, these restrictions prevent a necessary feature (see [6]), namely, sigmoidality at high thresholds.

C. The Sloping-Saturating Version of the Nizami-Schneider Equation

Nizami and Schneider [1] recognized such shortcomings, and were motivated to offer an alternative to the Sachs et al. [34] formulation for sloping-saturation, namely,

$$\begin{aligned} r(x) &= \gamma\left[\left(r_{\max}-r_s\right)\cdot\alpha_1(x)+r_s\right] \\ &\quad + (1-\gamma)\left[\left(r_{\max}-r_s\right)\cdot\alpha_2(x)+r_s\right] \\ &= \left(r_{\max}-r_s\right)\left[\gamma\,\alpha_1(x)+(1-\gamma)\alpha_2(x)\right]+r_s \end{aligned} \tag{11a}$$

where, defining $\zeta_{\mathrm{i}} = \lambda_{\mathrm{i}} / \left[2\ln\left(\left(100-c\right)/c\right)\right]$ and $\eta_{\mathrm{i}} = \varepsilon + \left(\lambda_{\mathrm{i}}/2\right)$, we further define

$$\left(1/\alpha_{\mathrm{i}}(x)\right) = 1 + e^{-\left(\frac{x-\eta_{\mathrm{i}}}{\zeta_{\mathrm{i}}}\right)} \quad \text{for } \mathrm{i}=1,2. \tag{11b}$$

Numerous exercises have demonstrated that Eq. (11a) fits well to sloping-saturating rate-level relations ([1], [2], [6]-[8], [13], [15], [16], [21]-[23]). However, the parameters to be fitted are now six in number: $r_{\max}$, r_s, ε, γ, λ_1, and λ_2. With six free parameters, the fit is no longer robust. Note well that six parameters also characterize a rate-level equation for auditory-nerve fibers published by Yates and used heavily by Yates and colleagues ([35], [36]). It was based upon saturating power-functions, like the Sachs et al. [34] equations. But Eq. (11a) fits better than the Yates et al. or Sachs et al. equations when the bend in the sloping-saturating plot is a sharp one.

For sloping-saturating neurons in the cat, the animal examined by Sachs and Abbas [5] and by Sachs et al. [34], the uncertainties of the parameters of Eq. (11a) can be somewhat mitigated by setting $r_s = 0$, because sloping-saturating neurons in cats seem to have very low firing rates (reviewed in [1], [6]). The same may not be true, however, of other species. Equation (11a) also fits adequately to “straight” rate-level relations [8], which may be considered as sloping-saturating relations with brief initial sections and extensive sloping-saturating sections [36]. Heil et al. [4] did not mention “straight” rate-level relations.

The observably excellent fit of the Nizami-Schneider double-sigmoid (Eq. (11a)) to sloping-saturation suggests that sloping-saturation is an artifact, caused by recording spikes simultaneously from two sigmoidally-saturating neurons with low spontaneous firing rates, one neuron having a notably higher threshold than the other. This would help to explain another observation, namely, that many sloping-saturating rate-level plots, unlike sigmoidal rate-level plots, do not reach a maximum firing rate at the highest intensity used in the experiment (typically 90-95 dB SPL). Artifactuality of sloping-saturation would account for a phenomenon that becomes apparent when reading the literature, namely, that sloping-saturating fibers represent startlingly different proportions of the auditory-nerve fibers from study to study, not just across-species, but even within a single species (reviewed in [2], [7]).

VI. Summary and Conclusions

In auditory neuroscience, it has long been thought that a well-fitting function of the root-mean-square (RMS) intensity of an applied single-frequency tone, a “rate-level” equation, would aid in the comprehension of the physical and physiological mechanisms of hearing. Heil, Neubauer, and Irvine [4] proposed an “improved” variation on a saturating power function published by Sachs and Abbas [5] as an auditory rate-level equation. Heil et al. [4] then abandoned their own equation, because it could not explain the observed spontaneous firing of auditory-nerve fibers, particularly (1) a correlation (alleged by Heil et al., but perhaps illusory) between spontaneous firing rate and the fiber's threshold, that is, the lowest tone intensity at which the fiber fires above its spontaneous rate, and (2) the existence of sub-spontaneous-rate firing, which is seen post-stimulus. Heil et al. [4] noted that their equation could be rewritten as a logistic, such as that of Nizami and Schneider [1] and Nizami [6]. Heil et al. [4] alleged that the Nizami-Schneider equation is equivalent to the Sachs and Abbas [5] equation. It is not. This is one of several egregious errors made by Heil et al. [4] which altogether make their "improvement" inconsequential. The Nizami-Schneider equation provides a viable alternative, but has been underused due to the ongoing fixation on the Sachs-Abbas equation, which has a crucial flaw: a fixed dynamic range for the firing of the auditory-nerve fiber.

The Nizami-Schneider formulation is advantageous in that it defines threshold such that firing rate just exceeds the spontaneous rate at threshold, allowing nonzero loudness at threshold, a phenomenon implied by experiment and by theory. Further, it is the only rate-level equation to include dynamic range as a parameter. The Nizami-Schneider equation was emphatically not modeled on the Sachs-Abbas equation. The latter even appears to be unoriginal, bearing a striking resemblance to an equation of Adams [24].

Heil et al. [4] allegedly used data from Nizami [6] to find a correlation between spontaneous firing rate and a threshold parameter of their equation. How Heil et al. [4] did so, from the limited data of Nizami [6] which was meant to serve other purposes, was not explained, and Heil et al.'s correlation coefficient is too small to suggest any correlation. This alleged correlation is important, because Heil et al. [4] used it as partial justification for abandoning their initial equation and replacing it with another, one based upon a new assumption about the spontaneous firing of auditory-nerve fibers, namely, that it is due to a mysterious "physiological" (i.e., internal) stimulus. Heil et al. [4] fail to mention that this gambit is not new; it dates at least to Zwislocki [25], whose work was later emulated concept-by-concept (and hence equation-by-equation) by Moore, Glasberg, and Baer [26], whose equations were, in turn, incorporated into a recent ANSI Loudness Standard. Further, the Heil et al. [4] newer equation predicts that the fiber will fire below its spontaneous rate at subzero stimulus intensities, the latter being impossible when stimulus intensity is expressed in the customary RMS units.

The newer Heil et al. [4] equation did not include spontaneous rate as a parameter. Heil et al. [4] compensated for this by stipulating that spontaneous rate is reached when the stimulus is absent, thereby creating a relation of spontaneous rate to threshold that they refer to as "emergent". Of course, it only "emerges" because of (1) the aforementioned stipulation, and (2) the notion that RMS intensity can be subzero. They excused the latter through an extraordinary claim: that their variable is *instantaneous* pressure, rather than the RMS pressure used by their progenitors, Sachs and Abbas [5].

Altogether, the Heil et al. [4] rate-level equation is not an "improvement". Their attempts failed, because of a problem that they showed no recognition of, and which goes unmentioned in the literature. That is, there are contradictory limits for the intensity called "threshold". This is reflected in a lack of agreement in the literature on how to discern "threshold". Effectively, Heil et al. [4] assumed that threshold occurred at $-\infty\ \mathrm{dB\,SPL}$. That situation is unrealistic. The notion of threshold at $-\infty\ \mathrm{dB\,SPL}$ is widely attributed to Swets [29], but Swets did not produce compelling evidence for it. The Nizami-Schneider equation avoids it, by assuming that threshold [intensity] corresponds to some firing rate just in excess of the spontaneous rate. In principle, this allows nonzero loudness at threshold.

Finally, some fibers *appear* to have rate-level plots which are "sloping-saturating", having a sharp bend in the middle, followed (with further increase in RMS stimulus amplitude) by an upper, lesser slope. Any "improved" rate-kevel function might be expected to fit such plots. One attempt was made by Sachs, Winslow, and Sokolowski [34], who modified the Sachs-Abbas equation. Heil et al. [4] largely ignored Sachs et al. [34]. Heil et al. [4] failed to mention that an extended Nizami-Schneider equation can fit sloping-saturating plots better than other proposed equations.

APPENDIX

It is necessary to correct a misconception that persists in the literature. Sachs and Abbas (1974) introduced their saturating power function without citing earlier use of it, implying that their own use was original. Subsequent authors, including Sachs and his various co-authors, cited Sachs and Abbas [5] as the equation's source. In the notation of Sachs and Abbas, the equation was

$$r(P)=\frac{R_m\left[d(P)\right]^N}{\theta+\left[d(P)\right]^N}+R_{\mathrm{SP}} \tag{A1}$$

([5], Eq. 2). Here, "*P* is sound pressure at the tympanic membrane" and "*d* is the amplitude of basilar-membrane displacement" ([5], p. 1839). R_{SP} is the neuron's spontaneous firing rate ([5], p. 1839), the equivalent of r_s in Eq (3); R_m ([5], p. 1839) is the equivalent of $r_{\max}-r_s$ in Eq (3). *N* was taken as 1.77, based on an argument provided by Sachs and Abbas.

Unfortunately, *Eq. (A1) did not originate with Sachs and Abbas [5]*, as will now be demonstrated. In 1971, William B. Adams showed that voltage-spike firing rate in the more sensitive of the two primary auditory afferents in each hearing organ of the Noctuid moth could be described by (in Adams's notation)

$$\text{response}=\frac{k\,bx}{1+bx} \tag{A2}$$

([24], 1971, Eq. (1)), where

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$$x \propto \left(\text{displacement}\right)^{1.7} + (\text{residual conductance}). \quad \text{(A3)}$$

Note immediately the word "displacement", referring to physical "displacement of the transduction region" ([24], p. 577). Note well the exponent of 1.7. Equation (A2) ([24], Eq. (1)), with Eq. (A3) substituted into it, differs little from what Sachs and Abbas published three years later [5]. Adams himself ([24], p. 575) in fact credited his equation for "response" to Loewenstein [37], for the generator potentials of Pacinian corpuscles. Loewenstein [37] indeed shows the equation as "Eq. 1", present also in Loewenstein's Figs. 6-8.

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