

We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

6,900

Open access books available

186,000

International authors and editors

200M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com



Lütkenhöner's „Intensity Dependence of Auditory Responses“: An Instructional Example in How Not To Do Computational Neurobiology

Lance Nizami
Independent Research Scholar
USA

1. Introduction

In „Threshold and beyond: modeling the intensity dependence of auditory responses“ (JARO 9, 2008, pp. 102-121), Dr. Bernd Lütkenhöner introduces us to a puzzle, namely, that responses to stimuli of low intensity appear to climb as the logarithm of the intensity, contrary to the expectation that they be linear with intensity. Towards solving that puzzle, Dr. Lütkenhöner has produced the latest in a long line of attempts by various authors to model „the gross response of the population of auditory nerve fibers“ in response to a pure tone (Lütkenhöner, p. 102). From his model, Dr. Lütkenhöner predicts linearity with intensity at low intensities, changing to linearity with log-intensity at higher stimulus intensities.

The present author is one of those who have contributed to this particular field of modeling (Nizami & Schneider, 1997; Nizami 2001, 2002, 2005a, 2005b), and was intrigued by what new insights Dr. Lütkenhöner might have to offer. However, substantial omissions and mistakes were found, which greatly reduce the value of Dr. Lütkenhöner's contribution. In particular, Lütkenhöner omits to mention the many earlier contributions towards modelling the firing of the whole auditory nerve or some portion thereof, so that his model escapes comparison to those of others. His computations use data taken from a variety of species, whose firing-rate characteristics are known to differ, such that his computations may describe no real species at all. Further, Dr. Lütkenhöner's equations do not account for the known variance of dynamic range across neurons, a crucial component of any model of mass neural firing. Indeed, he encourages the use of a discredited equation that cannot actually account for dynamic range variation, while ignoring a proven equation that can. Lütkenhöner also perpetuates the absurd notion of an infinitely low detection threshold for auditory stimuli. Finally, Lütkenhöner's derivations provide an equation of a form known to arise from circular logic. All of these errors are incontrovertible and render Dr. Lütkenhöner's work null and void. Altogether, Lütkenhöner's errors serve as a warning to those who attempt to compute the average neuronal response available from a mass of responding neurons, but serve the larger purpose of illustrating the folly of accepting conventional wisdom and frequently-cited papers on face value without delving deeply enough into the literature to achieve a professional understanding of a problem.

2. The Lütkenhöner model and its predecessors

2.1 Averaging of neuronal firing rates

The average firing rate of a pool of related neurons has historically been taken as the „signal“ that represents the outside world. That notion has been reinforced, for example, by recent cortical recordings which imply the use of „a code that is robust to perturbations, such as a rate code in which it is the average firing rate over large populations of neurons that carries information“ (London et al., 2010). But on average, no two neurons produce the same plot of firing rate as a function of the intensity of a given type of stimulus. To find the average firing rate of a *pool* of neurons, then, it is first necessary to find a rate-level function containing parameters which can be varied in order to represent the rate-vs.-intensity plot for individual neurons. Once such an equation is found, the „average“ neuronal response available from a mass of responding neurons can be obtained either by averaging modeled firing rates across neurons, or by analytically solving for the average of the actual equations. Dr. Lütkenhöner uses both methods. However, he omits any mention of earlier efforts, as if none exist.

2.2 The pioneering work of Schiaffino

In fact, averaging of stimulus-evoked firing of primary afferent sensory neurons has a long and rich history. The literature on hearing, in particular, shows progressive refinement over the years (Schiaffino, 1957; Barducci, 1961; Siebert, 1965; McGill & Goldberg, 1968; Goldstein, 1974; Howes, 1974, 1979; Lachs et al., 1984; Delgutte, 1987; Viemeister, 1988; Winslow & Sachs, 1988; Nizami & Schneider, 1997; Nizami, 2005b). That literature is worthy of a brief recapitulation. Schiaffino's model (1957) set the stage for all subsequent models. Ironically, Schiaffino did not rely upon properties of neuronal firing per se, which were not well-known at the time. Rather, he relied upon psychophysical results, as follows. He assumed that the absolute detection threshold for an auditory stimulus corresponded to the excitation of a single primary afferent auditory neuron, and that each psychophysical just-noticeable intensity increase corresponded to the firing of another neuron, such that the number of neurons activated by an increase of one unit of auditory intensity was the inverse of the size of the just-noticeable intensity increase. (Such cavalier assumptions would not, of course, be made today.) The just-noticeable intensity increase was known as a function of stimulus intensity for particular circumstances (and has since been found for stimuli of various durations and spectra), and so Schiaffino integrated its inverse with respect to intensity, obtaining the growth of the number of active fibers as a function of the stimulus intensity. He noted that squaring that quantity gave a curve congruent to psychophysical loudness curves established by psychologists. Note well Schiaffino's assumption (now quite unorthodox) that each neuron's contribution to loudness was the same. That assumption would not be made by subsequent others, once experimentalists had established that the firing rates of auditory primary afferents were themselves a monotonically increasing function of stimulus intensity. Nonetheless, by using mathematical integration to infer the growth of loudness from neuronal activity, Schiaffino laid the groundwork for all subsequent models of the dependence of loudness upon primary afferent firing. The above describes only the basics of Schiaffino's work. Barducci (1961) extended it to other frequencies by adding an arbitrary parameter to the number of active neurons.

Since Schiaffino's time it has become well-established that single primary afferent auditory neurons in all species studied can be characterized by four properties: their spontaneous

rate in the absence of any stimuli, their saturation (maximum) rate beyond which rate cannot increase regardless of stimulus intensity, their threshold intensity at which firing rate (on average) increases beyond spontaneous rate, and their dynamic range, defined as the intensity range between threshold intensity and saturation intensity. There is a different, psychophysical dynamic range for the whole animal. As noted by Lawrence (1965, p. 159), „The [psychophysical] dynamic range expresses the extent of rising intensities over which hearing takes place, but the upper limit is difficult to define“. Lawrence (1965) describes the upper limit as that intensity at which the sensation of loudness mingles with the sensation of feeling. That limit appears to be constant despite the fact that the threshold for detection of auditory stimuli (the absolute detection threshold) varies with the frequency of a pure tone (Licklider, 1951/1966). Lawrence (1965, p. 161) notes that Licklider's paper implies human psychophysical dynamic ranges of 90 decibels for 100 Hz tones and for 10,000 Hz tones, and 120 decibels for 1,000 Hz tones.

2.3 The dynamic range problem

These ranges are an object of puzzlement, for the following reasons. Humans are not used for studying the properties of the primary afferent auditory neurons. On the contrary, the mammal whose peripheral auditory neurons we know best is the cat. Individual primary afferent auditory neurons of the cat, which leave the periphery by way of the 8th (auditory) nerve, typically have a range from threshold to saturation of only 14-40 decibels (e.g. Kiang et al., 1965). Thus, theories of neuronal function that hope to capture the full behavioral range of hearing in the cat (and by extension, in man) have to stipulate how neurons of such limited dynamic range can encode intensity over the full behavioral range. One approach has been to assume that auditory stimulus intensity is proportional to activity in the whole auditory nerve (e.g., Schiaffino, 1957; Barducci, 1961; McGill & Goldberg, 1968; Goldstein, 1974; Howes, 1974, 1979; Lachs et al., 1984). The general argument for this type of model is as follows for a pure tone. As the tone intensity increases from the absolute psychophysical (behavioral) detection threshold for the tone, neurons serving the region of the hearing organ (the organ of Corti) at and nearby the locus of its maximum physical displacement increase their rate of firing voltage spikes until they reach their saturation firing rate. However, as the tone's intensity increases still further, there is a lateral spread of the tone-evoked physical movement of the organ of Corti, such that neurons adjacent to the point of maximal physical displacement are recruited (e.g., Howes, 1974, based on Katsuki et al., 1962; Pfeiffer & Kim, 1975). Thus, increasing the tone's intensity means an increase in the firing rate of neurons that are already responding, and an increase in the number of responding neurons (see Whitfield, 1967). The total number of voltage spikes elicited by the stimulus will therefore continue to increase, in such „whole-nerve“ models, because the zone of significant physical displacement of the organ of Corti will continue to widen as the tone's intensity rises.

There is evidence, however, that a wide range of intensity can be encoded under conditions that prohibit the recruitment of unsaturated neurons. That is, Viemeister (1983) used a high-intensity notched masking noise to potentially saturate the firing rates of neurons that were most responsive to tones below 6,000 Hz and above 14,000 Hz, thus eliminating the possibility that such neurons could contribute to encoding intensity changes for tones below 6,000 Hz or above 14,000 Hz. Human subjects were required to discriminate intensity

changes in a noise whose spectrum of component frequencies spanned the range of 6,000-14,000 Hz. The subjects were able to do so, suggesting that spread of excitation beyond the 6,000-14,000 Hz band was unnecessary for the growth of loudness of the 6,000-14,000 band of noise. One way in which this could happen is for neurons within any limited contiguous span of the organ of Corti to have different firing thresholds and/or different neuronal dynamic ranges. Such a simple system may be realized, for example, in some species of moths, for which there are only two primary auditory afferents, having different thresholds but similar dynamic ranges, which therefore partially overlap (e.g., Perez & Coro, 1985). There is other psychoacoustic evidence which suggests that a small region surrounding the point of maximal stimulus-driven physical displacement on the organ of Corti can encode a large dynamic range. For example, Hellman (1974) found that using a masking noise to presumably remove the neural firing contributions of neurons of greatest sensitivity above 250 Hz does not prevent the normal growth of the loudness of a 250 Hz tone. Thus, any model of pooled neuronal firing must be restricted to a limited portion of the organ of Corti.

2.4 What species for Lütkenhöner?

The most sophisticated model of pooled neuronal firing is that of Nizami and Schneider (1997). It was concerned with the firing of the neurons serving a limited region of the organ of Corti centered on the point of maximal displacement for an 8,000 Hz tone in the cat. The Nizami and Schneider model will be described below in the course of examining Lütkenhöner's model. However, there is already one glaring difference between Dr. Lütkenhöner's model and the others cited here, a difference which arises early in Lütkenhöner's paper. That is, that all of the other models are specific to particular species (usually the cat; but see for example Howes, 1974, for the macaque), whereas Lütkenhöner fails to state what species his computations apply to, as if they apply to all. In practice, he bases his computations upon a hodgepodge of data taken from cats, guinea pigs, and alligator lizards, species whose firing-rate characteristics are well known to substantially differ.

3. Problems with the Lütkenhöner model: dynamic ranges of afferents

Dr. Lütkenhöner focuses his derivations on the average neuronal firing behavior near threshold. However, his various mathematical summations fail to account for the known difference in the distributions of thresholds and of dynamic ranges of the individual afferents. Those variabilities significantly affect average rate-level behavior (see Nizami & Schneider, 1997, and its predecessors listed above). In turn, rate-level behavior affects discriminability, as quantified in Signal Detection Theory models (e.g. Nizami & Schneider, 1997; Nizami 2003, 2005a, 2005b). Hence, threshold and dynamic range affect discriminability, making them of paramount importance. Regarding thresholds, Lütkenhöner states that "there is insufficient information about the true sensitivity distribution of the auditory neurons" (Lütkenhöner, p. 116). However, the distribution of thresholds across primary auditory afferents is well-characterized for the cat (reviewed in Nizami & Schneider, 1997), guinea pig, macaque (e.g., Katsuki et al., 1962), and several other mammals. The distribution of dynamic ranges across neurons is also well-characterized for primary auditory afferents (see the review in Nizami & Schneider, 1997, for the cat). Thus Lütkenhöner has failed to incorporate important data that is readily available.

4. Problems with the Lütkenhöner model: an equation having a fixed dynamic range

Let us examine if and how dynamic range actually appears in Lütkenhöner's formulation. We might expect dynamic range to be defined in terms of the discriminability afforded by a neuron's rate-level relation. In fact, that has been done just once (Nizami, 2005a). In the remainder of the literature, dynamic range was quantified as the difference between a threshold intensity for evoked firing, and an intensity at which firing rate saturates. Those dynamic-range endpoints have in turn been defined in terms of the neuron's minimum (i.e. actual spontaneous) firing rate R_{\min} spikes/s and its maximum (i.e. actual „saturation“) firing rate R_{\max} spikes/s, according to variations on any of four different schemes (reviewed in Nizami, 2002).¹ Indeed, such measurement schemes led originally to the conclusion that dynamic ranges vary significantly from neuron to neuron (e.g., Evans & Palmer, 1980).

Ironically, those same schemes prevent Dr. Lütkenhöner's model from ever accounting for differences in dynamic range, and that is important, because a model that cannot account for differences in dynamic range cannot ultimately provide a good fit to rate-intensity data from the neuron, in which case any forthcoming „average neural response“ will be inaccurate. Consider the following. Lütkenhöner's chosen rate-level function was a personal customization of the rate-level function chosen by Sachs and Abbas (1974) to describe the response of single primary auditory afferents in cats exposed to pure tones. The latter equation belongs to a class of equations called saturating power functions. With R being spike firing rate, P being RMS (root-mean-square) sound-pressure-level, and k and α being positive parameters that can be obtained by regression on actual rate-level data, the saturating power functions take the form

$$R(P) = R_{\max} \frac{(P/P_0)^\alpha}{(P/P_0)^\alpha + k} \quad (1)$$

Because intensity I is proportional to P^2 , intensity can be used in place of P without loss of generality. Now, the above equation can be inverted, producing sound-pressure-level P as a function of firing rate. From there, it is easily proven that for a fixed α , the equation $R(P)$ represents a *fixed dynamic range* (Nizami, 2002). That fixed range can be expressed by formulae, according to whichever of the four popular dynamic-range schemes was used (*ibid.*).

One solution to this problem of an inadvertently constant dynamic range in rate-intensity equations is to allow dynamic range to vary, by building it into a rate-intensity equation as a parameter. Such a parameter is not present in earlier equations for auditory single-unit

¹ Those schemes depend upon arbitrarily-chosen parameters a and b , where $0 < a, b < 50$, as follows. In Scheme 1, threshold firing rate is $\frac{a}{100} (R_{\max} - R_{\min})$ and saturation firing rate is

$\left(1 - \frac{b}{100}\right) (R_{\max} - R_{\min})$. In contrast, Scheme 2 uses $\frac{a}{100} (R_{\max} - R_{\min}) + R_{\min}$ and

$\left(1 - \frac{b}{100}\right) (R_{\max} - R_{\min}) + R_{\min}$ respectively; Scheme 3 uses $R_{\min} \left(1 + \frac{a}{100}\right)$ and $R_{\max} \left(1 - \frac{b}{100}\right)$; and

finally, Scheme 4 uses $R_{\max} \frac{a}{100}$ and $R_{\max} \left(1 - \frac{b}{100}\right)$. Schemes 1 and 4 have obvious problems; Scheme 2 is the most popular one (see Nizami, 2002).

firing rate (e.g., Schiaffino, 1957; Barducci, 1961; McGill & Goldberg, 1968; Goldstein, 1974; Howes, 1974; Sachs & Abbas, 1974; Lachs et al., 1984; Sachs et al., 1989; Yates et al., 1990). However, Nizami and Schneider (1997) presented such an equation:

$$r(x; \varepsilon, \lambda, r_{\max}, r_s) = \frac{r_{\max} - r_s}{1 + \left(\frac{100 - c}{c}\right)^{1 - \left[2\left(\frac{x - \varepsilon}{\lambda}\right)\right]}} \quad (2)$$

where x = intensity in decibels SPL,
 ε = threshold for stimulus-evoked firing, in decibels SPL,
 λ = dynamic range in decibels,
 r_{\max} = saturation firing rate in spikes/s,
 r_s = spontaneous firing rate in spikes/s.

The actual derivation of Eq. 2 appeared later (Nizami, 2001, 2002). Equation 2 describes a symmetric, sigmoidal (S-shaped) plot. Equation 2 incorporates two assumptions: first, that the neuron's firing rate „at threshold“ is characterized by

$$r(x = \varepsilon) = \frac{c}{100} (r_{\max} - r_s) + r_s, \quad (3)$$

and second, that the neuron's saturation firing rate obeys

$$r(x = \varepsilon + \lambda) = \frac{100 - c}{100} (r_{\max} - r_s) + r_s \quad (4)$$

(Footnote 1, Scheme 2, with $a = b = „c“$), all for $c = 2$. Equation 2 fits typical rate-intensity plots quite well (see Nizami, 2002, 2005a) using $c = 2$, with the parameter values obtained through least-squares fitting of equation to data being very close to those estimated [through observation] by the persons who obtained the rate-intensity data in the first place. Indeed, fitted and estimated values mutually diverge more when using other possible values of c , namely $c = 1$, $c = 5$, or $c = 10$ (Nizami, 2002).

In a broad variety of species, including those that Dr. Lütkenhöner uses as sources of data, there are a greater or lesser percentage of the examined primary afferent auditory neurons whose rate-intensity plots do not follow a sigmoid. Instead, the plots show a fairly sharp mid-way bend to a shallower slope, presumably followed by eventual saturation beyond the highest stimulus intensities (90-95 decibels sound-pressure-level [SPL]) that were employed (e.g., Sachs & Abbas, 1974; Palmer & Evans, 1979; Sachs et al., 1980; Winter et al., 1990; Ohlemiller et al., 1991; Temchin & Moushegian, 1992; Richter et al., 1995; Koppl & Yates, 1999; Plontke et al., 1999; Yates et al., 2000; Imaizumi & Pollack, 2001). These neurons acquired the name „sloping-saturating“. Nizami and Schneider (1997) found that sloping-saturating rate-intensity plots were fitted well by the equation

$$r_{SS}(x; \varepsilon, \lambda_1, \lambda_2, r_{\max}, r_s) = \gamma \cdot r(x; \varepsilon, \lambda_1, r_{\max}, r_s) + (1 - \gamma) \cdot r(x; \varepsilon, \lambda_2, r_{\max}, r_s) \quad (5)$$

where γ is a fitted parameter. Equation 5 has six fitted parameters, but for the cat we can set the spontaneous rate to zero, reducing the number of fitted parameters to five. Yates produced an equation in six parameters which Yates and others fitted to sloping-saturating plots (e.g., Yates, 1990; Richter et al., 1995; Koppl & Yates, 1999; Yates et al., 2000), but Eq. 5 fits more closely to the bend in the plot, as can be seen by comparing the work of Yates et al. to the fit of Eq. 5 (see for example Nizami & Schneider, 1997; Imaizumi & Pollack, 2001; Nizami, 2002, 2005a). The same goes for the Sachs et al. (1989) equation in five parameters. Equation 5 is not meant to represent any underlying mechanics, unlike the Sachs and Abbas (1974) equation used by Dr. Lütkenhöner, and its successors, the equations of Sachs et al. (1989) and of Yates et al. (1990). All of those equations in fact encapsulate an alleged relation of the shape of the sloping-saturating firing-rate plot to the plot of the intensity-dependence of the mechanical vibration of the organ of Corti, a relation proven illusory (e.g., Palmer & Evans, 1979; Palmer & Evans, 1980). Also, Equation 5 does show saturation (levelling off) at sound pressure levels that lie beyond the range of the data. Earlier models of collected neuronal firing rates (Schiaffino, 1957; Barducci, 1961; McGill & Goldberg, 1968; Goldstein, 1974; Howes, 1974; Lachs et al., 1984; Delgutte, 1987; Viemeister, 1988; Winslow & Sachs, 1988) did not account for neurons whose rate-intensity plots are sloping-saturating. Equations 2 and 5 can help us determine the rate-intensity relation for an „average“ neuron, as follows. Given a mass of primary afferent auditory neurons, the threshold, dynamic range, spontaneous firing rate, and saturation firing rate will vary from neuron to neuron. That variability can be quantified by measuring those characteristics over a large sample of neurons. The characteristics form probability density functions. If the neuronal characteristics appear to be mutually independent of each other – which can be ascertained by plotting one against another and looking for correlations – then the mean firing rate of an ensemble of neurons having sigmoidal rate-intensity plots is given by

$$\int_{\min(\varepsilon)}^{\max(\varepsilon)} \int_{\min(\lambda)}^{\max(\lambda)} \int_{\min(r_{\max})}^{\max(r_{\max})} \int_{\min(r_s)}^{\max(r_s)} [r(x; \varepsilon, \lambda, r_{\max}, r_s) \cdot p(\varepsilon) \cdot p(\lambda) \cdot p(r_{\max}) \cdot p(r_s)] dr_s dr_{\max} d\lambda d\varepsilon \quad (6)$$

where $p(\varepsilon)$ = probability density function for threshold,
 $p(\lambda)$ = probability density function for dynamic range,
 $p(r_{\max})$ = probability density function for saturation firing rate,
 $p(r_s)$ = probability density function for spontaneous firing rate.

A similar expression applies for sloping-saturating neurons. Equation 6 might be solvable analytically, but if not, it can easily be integrated numerically (see Nizami & Schneider, 1997). This method offers greater comprehensiveness than merely averaging firing rates over a few „representative“ neurons, as was done elsewhere (e.g., Siebert, 1965; Goldstein, 1974; Howes, 1974; Viemeister, 1983; Winslow & Sachs, 1988).

The point is that there were neuronal rate-intensity equations, and the methodology of how to use them to obtain „average“ rate-intensity functions for pools of neurons, that were available to Dr. Lütkenhöner and that could have been used to account for empirical variability in threshold and dynamic range. But these investigative tools were not used, or even mentioned, by Lütkenhöner.

5. Problems with the Lütkenhöner model: infinitely low threshold

Dr. Lütkenhöner's model encourages the continuing needless use of the inflexible saturating-power-function. But that is not all. Lütkenhöner's model also perpetuates an outdated notion, as follows. Lütkenhöner cites Swets (1961) and states that „In accordance with signal detection theory, the model denies the existence of a threshold“ (Lütkenhöner, p. 102). This act of denial was considered so important that it was mentioned in Lütkenhöner's abstract. But the notion of no threshold is counterintuitive. Lütkenhöner's use of it compels a reexamination of his source, the paper of Swets (1961). Swets' paper was a review of Signal Detection Theory (here denoted SDT) as it was laid down at the time, including the key SDT concept 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 upon the ratio of the likelihood of Signal+Noise to the likelihood of Noise alone. That likelihood ratio obeys two distributions – one for Signal+Noise and one for Noise – and the listener places their hypothetical decision-making criterion somewhere along that likelihood-ratio continuum. An infinitely low threshold is possible, but only because the theoretical distributions involved have infinitely long tails.

Regarding threshold, Swets (1961) reviewed 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 „concerning the processes underlying these data“ (Swets, p. 175). Swets' words were often unclear, and his analysis was long and complicated and defies brief synopsis. His conclusions were hardly firm; in fact, Swets was oddly equivocal. He first noted that one of the models that he examined fit none of the data, that two of the models fit some of the data, 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, but that SDT did too. In conclusion, Swets stated that „The outcome is that, as far as we know, there may be a sensory threshold“ (p. 176). He then started his next paragraph with „On the other hand, the existence of a sensory threshold has not been demonstrated“ (*ibid.*). This turnabout seems especially odd in light of some shortcomings of SDT that were noted by Swets, in particular 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“ (p. 172). That finding has been replicated many times over; for intensity discriminability, for example, see deBoer (1966), Raab and Goldberg (1975), Schacknow and Raab (1976), Green and Swets (1988), Bernstein and Raab (1990), Buus (1990), Nizami and Schneider (1997), and Nizami (2005b), among others. In sum, Swets (1961) did not produce compelling evidence of an infinitely low threshold, thus leaving no reason to reject the notion, as expressed by Hellman and Zwislocki (1961, p. 687), that “The threshold of audibility is a natural boundary condition which cannot be eliminated”.

6. Problems with the Lütkenhöner model: a function containing a circular argument

Dr. Lütkenhöner's derivations lead to one mathematical case, presented on p. 112 of his paper, which resembles an equation by Zwislocki (1965). Lütkenhöner's version was obtained by „an appropriate normalization of both the intensity and the loudness scale“ (Lütkenhöner, p. 112). Lütkenhöner notes this equation's similarity to several of his own equations for the normalized auditory firing rate. Unfortunately, as revealed in a recent proceeding (Nizami, 2009), Zwislocki's original equation was based upon circular reasoning. Hence circular reasoning may also underlie Lütkenhöner's equations as well. It

may be worthwhile, for the reader's benefit, to briefly reiterate the problems with the Zwillocki derivation, as follows.

Experiments led to the notion that the loudness of an auditory stimulus at its absolute detection threshold is not zero, contrary to traditional assumptions (e.g., Buus et al., 1998; Buus & Florentine, 2001). Nonzero threshold loudness was predicted from theory by Zwillocki (1965), and by Moore et al. (1997) in an update of Zwillocki's paper. The Moore et al. loudness equation actually appears in a modern standard for loudness, ANSI Standard S3.4-2007.

6.1 Zwillocki's (1965) derivation

Zwillocki (1965) used L to represent loudness and P to represent RMS pressure amplitude. Zwillocki proposed that for a physiologically normal listener attending to a single pure tone of intensity > 50 dB SPL, loudness obeys $L = K P^{2\theta}$ where $\theta > 0$. The parameter K is found by curvefitting of empirical loudnesses (obtained through magnitude estimation procedures) to the loudness equation. At "sufficiently high sound-pressure levels" P (Zwillocki, p. 84), but for stimuli whose spectra still lie within the critical band f to $f+CB$, Zwillocki proposed that

$$L = K \left(\sum_f^{f+CB} P^2 \right)^\theta. \quad (7)$$

For a pure tone S („ S “ indicating „signal“) centered frequency-wise in a noise band N , $L = K (P_S^2 + P_N^2)^\theta$. Here the P 's represent „effective“ tone or noise pressures, „effective“ because the vibrations of the organ of Corti which are tone-evoked or noise-evoked will physically interfere with each other. Zwillocki then made a bold move: noting that listeners can selectively ignore noise, Zwillocki imagined the loudness of the tone-in-noise as the total loudness minus the noise loudness. The noise loudness was described as $L_N = K P_N^{2\theta}$ so that tone loudness was $L_S = K [(P_S^2 + P_N^2)^\theta - P_N^{2\theta}]$. Once again, Zwillocki imagined a total stimulus spectrum lying within one single critical band, so that other critical bands contribute nothing to the loudness.

Zwillocki proceeded to assume that there was a „physiological noise“ which behaved like a physical masking noise, one that the listener could *not* ignore. Zwillocki attributed the existence of an absolute detection threshold to that physiological noise. Representing that internal noise using the subscript NI , Zwillocki then imagined the total Noise sound pressure, P_N^2 , to be the sum of the internal-noise sound pressure and the external-noise sound pressure, altogether $P_N^2 = (P_{NI} + P_{NE})^2 = P_{NI}^2 + P_{NE}^2$. Zwillocki failed to note that the term $2 P_{NI} P_{NE}$ is zero when, presumably, P_{NI} and P_{NE} are independently drawn from zero-mean Gaussian distributions (see for example Green, 1960, or deBoer, 1966).

According to Zwillocki (1965), then, the total loudness of a pure tone embedded in noise is

$$L = K \left[\left(P_S^2 + P_{NI}^2 + P_{NE}^2 \right)^\theta - \left(P_{NI}^2 + P_{NE}^2 \right)^\theta \right]. \quad (8)$$

Without the external noise, tone loudness is

$$L = K \left[\left(P_S^2 + P_{NI}^2 \right)^\theta - \left(P_{NI}^2 \right)^\theta \right]. \quad (9)$$

Zwislocki then calculated the power of the external noise that would be equivalent to that of the imagined internal physiological noise. Using T to denote tone threshold, $P_S = P_T$ at the tone's absolute detection threshold *in quiet*. Then Zwislocki declared that $P_{NI}^2 = 2.5 P_T^2$. No proof was provided for that equality. In the absence of external noise, then, $L_S = K [(P_S^2 + 2.5 P_T^2)^\theta - (2.5 P_T^2)^\theta]$, so that $L_S = K [(3.5 P_T^2)^\theta - (2.5 P_T^2)^\theta]$ at the tone's absolute detection threshold. Thus, according to Zwislocki, the tone has nonzero loudness at its absolute detection threshold in quiet.

Zwislocki's conclusion depended crucially upon including P_{NI}^2 in the subtracted term in Eq. (3). It allows zero tone loudness when there is no tone ($P_S^2 = 0$). In so doing, Zwislocki violates his own assumption that the „physiological noise“ cannot be ignored by the listener. If that assumption is held to, then the internal noise cannot be included in the subtracted term. However, Zwislocki acted as if internal noise was a kind of *external* noise that appeared only when the tone appeared. Zwislocki's approach is truly extraordinary. Effectively, Zwislocki's pure tone carries a noise of fixed energy that masks the tone's own energy, creating an absolute detection threshold.

If this point is not yet clear, consider an expansion of $L_S = K [(P_S^2 + P_{NI}^2)^\theta - P_{NI}^{2\theta}]$ in a binomial series:

$$\begin{aligned}
 L &= K \left(P_{NI}^{2\theta} + \theta P_{NI}^{2(\theta-1)} P_S^2 + \frac{\theta(\theta-1)}{2!} P_{NI}^{2(\theta-2)} P_S^{2(2)} \right. \\
 &\quad \left. + \frac{\theta(\theta-1)(\theta-2)}{3!} P_{NI}^{2(\theta-3)} P_S^{2(3)} + \dots - P_{NI}^{2\theta} \right) \\
 &= K \left(\theta P_{NI}^{2(\theta-1)} P_S^2 + \frac{\theta(\theta-1)}{2!} P_{NI}^{2(\theta-2)} P_S^{2(2)} \right. \\
 &\quad \left. + \frac{\theta(\theta-1)(\theta-2)}{3!} P_{NI}^{2(\theta-3)} P_S^{2(3)} + \dots \right). \tag{10}
 \end{aligned}$$

The tone and internal-noise pressure components are clearly inseparable.

In sum, Zwislocki (1965) imposed an absolute detection threshold upon a pure tone (and hence incorporated a threshold tone loudness) by making an „internal“ noise inseparable from overall loudness. That is, in an act of patent circular logic, Zwislocki *assumed* a nonzero tone loudness at tone-detection threshold.

6.2 The Moore et al. (1997) derivation

In 1997, Moore et al. published an updated version of Zwislocki's book chapter. Their model concerned the loudness of stimuli per equivalent rectangular bandwidth (ERB), their own version of Zwislocki's critical band. Moore et al. called it the „specific“ loudness, denoted N' . The specific loudness was imagined as a function of a stimulus-evoked internal excitation E (in power units). As done by Zwislocki (1965), the tone was called „signal“, hence the tone-evoked excitation was E_{SIG} . Similarly, the peak excitation from a pure tone „at absolute threshold“ was called E_{THRQ} . Omitting several steps, the specific loudness for a pure tone in the absence of an external masking noise was

$$N' = C \left(\frac{2E_{SIG}}{E_{SIG} + E_{THRQ}} \right)^{1.5} \left[(GE_{SIG} + A)^\theta - A^\theta \right]. \tag{11}$$

„At threshold“ $E_{SIG} = E_{THRQ}$ and hence $N'_{THRESHOLD} = C [(GE_{THRQ} + A)^{\alpha} - A^{\alpha}]$, which exceeds zero. Thus Moore et al., like Zwislocki, concluded that a pure tone in quiet has nonzero loudness at absolute detection threshold.

Note the remarkable similarity of Eq. 11 to Eq. 9, Zwislocki's (1965) equation for tone loudness in quiet. This similarity suggests that Moore et al. followed the same circular logic that was used by Zwislocki. After all, Moore et al.'s paper was patterned after Zwislocki's. Their „loudness per ERB“ is equivalent to Zwislocki's loudness for the spectrum falling within a critical band; that is, Moore et al. and Zwislocki sought to quantify the same thing. Both Moore et al. and Zwislocki assumed power laws for loudness. Moore et al. effectively adopted Zwislocki's „internal noise“, a noise that is ignorable but somehow not ignorable, making tone loudness equal to zero when the tone is absent but inducing nonzero tone loudness „at threshold“ when the tone is present. Overall, then, Moore et al. assumed, rather than proved, nonzero tone loudness at the tone's absolute detection threshold.

6.3 The origin of the error

What is the ultimate origin of the circular logic used by Zwislocki (1965) and Moore et al. (1997)? The answer is not obvious. In seeking an answer, we might note that Zwislocki (1965) and Moore et al. (1997) started with a particular assumption, that is, that there is such a thing as a constant „threshold loudness“. However, two phenomena suggest that such an approach is spurious. First, magnitude estimates of loudness are distributed rather than constant (e.g., Stevens, 1956; McGill, 1960; Hellman & Zwislocki, 1963; Luce & Mo, 1965; Poulton, 1984; Hellman & Meiselman, 1988). There is thus an „average loudness“, rather than a constant loudness, for a given intensity of any particular stimulus. Similarly, absolute detection threshold itself is operationally defined probabilistically, using psychometric functions which illustrate the percentage of the time that a stimulus is heard as a function of the stimulus intensity. Thus there is no fixed stimulus „at threshold“.

7. Conclusions

Dr. Lütkenhöner's computations of the average neuronal response available from the mass of responding auditory primary afferents fails to account for two crucial factors, the across-neuron variability of threshold and of dynamic range. Attempts to incorporate dynamic-range variability would fail irregardless, because dynamic range cannot be incorporated as a variable in the saturating power function that Lütkenhöner uses; that equation has a fixed dynamic range. There is an equation in the auditory literature that incorporates dynamic range as a parameter, but Lütkenhöner ignores that equation. Further, Dr. Lütkenhöner perpetuates the outdated notion of an infinitely low detection threshold. Finally, he notes the similarity of his equations to an equation used by Zwislocki (1965), but the latter equation arose from circular logic, implying that Lütkenhöner's equations also arise from circular logic. These errors are by no means trivial and do not appear to be correctable within Dr. Lütkenhöner's computational framework. They cast serious doubt on the accuracy of his computations and stand as a warning to the computational neurobiologist who seeks to further understand the progression of massed neuronal firing rate with intensity. The errors committed by Lütkenhöner also highlight the need for very careful choices of the equations used to describe single-neuron firing rates. More broadly, Lütkenhöner's mistakes derived from using equations and concepts which are outdated but which remain prominent simply because they have been cited many times in the literature.

Unfortunately, as this critique of Dr. Lütkenhöner's work illustrates, popularity is not a substitute for correctness.

8. Acknowledgements

Professor Claire S. Barnes of Emory University provided valuable insights during the proofreading of this paper. Thanks also to the editorial staff of INTECH for their patient proofreading and especially to Prof. Katarina Lovrecic for her courteous correspondence.

9. References

- ANSI Standard S3.4-2007, *American National Standard- Procedure for the Computation of Loudness of Steady Sounds*, Acoustical Society of America, Melville, NY, USA.
- Barducci, I. (1961). Loudness function and differential sensitivity of intensity, *Proceedings of the 3rd International Congress on Acoustics, Vol. 1*, pp. 86-88, ASIN B000UG1GM0, Stuttgart, Germany, 1959, Elsevier, New York.
- Bernstein, R.S. & Raab, D.H. (1990). The effects of bandwidth on the detectability of narrow- and wideband signals, *Journal of the Acoustical Society of America*, 88, 5, 2115-2125, ISSN 0001-4966.
- Buus, S. (1990). Level discrimination of frozen and random noise, *Journal of the Acoustical Society of America*, 87, 6, 2643-2654, ISSN 0001-4966.
- Buus, S. & Florentine, M. (2001). Growth of loudness in listeners with cochlear hearing losses: recruitment reconsidered, *Journal of the Association for Research in Otolaryngology*, 3, 2, 120-139, ISSN 1525-3961.
- Buus, S., Musch, H. & Florentine, M. (1998). On loudness at threshold, *Journal of the Acoustical Society of America*, 104, 1, 399-410, ISSN 0001-4966.
- deBoer, E. (1966). Intensity discrimination of fluctuating signals, *Journal of the Acoustical Society of America*, 40, 3, 552-560, ISSN 0001-4966.
- Delgutte, B. (1987). Peripheral auditory processing of speech information: implications from a physiological study of intensity discrimination, In: *The Psychophysics of Speech Perception*, M.E.H. Schouten (Ed.), pp. 333-353, Dordrecht, ISBN 902473536X, Nijhoff, Holland.
- Evans, E.F. & Palmer, A.R. (1980). Relationship between the dynamic range of cochlear nerve fibres and their spontaneous activity, *Experimental Brain Research*, 40, 1, 115-118, ISSN 0014-4819.
- Goldstein, J.L. (1974). Is the power law simply related to the driven spike response rate from the whole auditory nerve?, In: *Sensation and Measurement*, H.R. Moskowitz, B. Scharf & J.C. Stevens (Eds.), pp. 223-229, D. Reidel Pub. Co., Dordrecht-Holland, ISBN 9027704740, Boston, MA, USA.
- Green, D.M. (1960). Auditory detection of a noise signal, *Journal of the Acoustical Society of America*, 32, 1, 121-131, ISSN 0001-4966.
- Green, D.M. & Swets, J.A. (1988). *Signal Detection Theory and Psychophysics*, Peninsula Publishing, ISBN 0-932146-23-6, Los Altos, CA, USA.
- Hellman, R.P. (1974). Effect of spread of excitation on the loudness function at 250 Hz, In: *Sensation and Measurement*, H.R. Moskowitz, B. Scharf & J.C. Stevens (Eds.), pp. 241-249, D. Reidel Pub. Co., Dordrecht-Holland, ISBN 9027704740, Boston, MA, USA.

- Hellman, R.P. & Meiselman, C.H. (1988). Prediction of individual loudness exponents from cross-modality matching, *Journal of Speech & Hearing Research*, 31, 4, 605-615, ISSN 0022-4685.
- Hellman, R.P. & Zwislocki, J.J. (1961). Some factors affecting the estimation of loudness, *Journal of the Acoustical Society of America*, 33, 5, 687-694, ISSN 0001-4966.
- Hellman, R.P. & Zwislocki, J.J. (1963). Monaural loudness function at 1,000 cps and interaural summation, *Journal of the Acoustical Society of America*, 35, 6, 856-865, ISSN 0001-4966.
- Howes, W. (1974). Loudness function derived from data on electrical discharge rates in auditory-nerve fibers, *Acustica*, 30, 5, 247-259, ISSN 0001-7884.
- Howes, W. (1979). Loudness of steady sounds - a new theory, *Acustica*, 41, 5, 277-320, ISSN 0001-7884.
- Imaizumi, K. & Pollack, G.S. (2001). Neural representation of sound amplitude by functionally different auditory receptors in crickets, *Journal of the Acoustical Society of America*, 109, 3, 1247-1260, ISSN 0001-4966.
- Katsuki, Y., Suga, N. & Kanno, Y. (1962). Neural mechanism of the peripheral and central auditory system in monkeys, *Journal of the Acoustical Society of America*, 34, 9B, 1396-1410, ISSN 0001-4966.
- Kiang, N.Y.-S., Watanabe, T., Thomas, E.C. & Clark, L.F. (1965). *Discharge Patterns Of Single Fibers In The Cat's Auditory Nerve*, MIT Press, ISBN 0262110164, Cambridge, MA, USA.
- Koppl, C. & Yates, G. (1999). Coding of sound pressure in the barn owl's auditory nerve, *Journal of Neuroscience*, 19, 21, 9674-9686, ISSN 0270-6474.
- Lachs, G., Al-Shaikh, R., Bi, Q., Saia, R.A. & Teich, M.C. (1984). A neural-counting model based on physiological characteristics of the peripheral auditory system. 5. Application to loudness estimation and intensity discrimination, *IEEE Transactions on Systems Man & Cybernetics*, SMC-14, 6, 819-836, ISSN 0018-9472.
- Lawrence, M. (1965). Dynamic range of the cochlear transducer, *Cold Spring Harbor Symposia on Quantitative Biology*, 30, 159-167. ISSN 0091-7451.
- Licklider, J.C.R. (1951/1966). Basic correlates of the auditory stimulus, In: *Handbook Of Experimental Psychology*, S.S. Stevens (Ed.), pp. 985-1039, Wiley, ASIN B000H4HIFE, New York, NY, USA.
- London, M., Roth, A., Beeren, L., Häusser, M. & Latham, P.E. (2010). Sensitivity to perturbations *in vivo* implies high noise and suggests rate coding in cortex, *Nature*, 466, 7302, 123-127, ISSN 0028-0836.
- Luce, R.D. & Mo, S.S. (1965). Magnitude estimation of heaviness and loudness by individual subjects: a test of a probabilistic response theory, *British Journal of Mathematical and Statistical Psychology*, 18, 2, 159-174, ISSN 0007-1102.
- Lütkenhöner, B. (2008). Threshold and beyond: modeling the intensity dependence of auditory responses, *Journal of the Association for Research in Otolaryngology*, 9, 1, 102-121, ISSN 1525-3961.
- McGill, W. (1960). The slope of the loudness function: a puzzle, In: *Psychological Scaling: Theory and Applications*, H. Gulliksen & S. Messick (Eds.), pp. 67-81, Wiley, ASIN B0000CKP1Q, New York, NY, USA.

- McGill, W.J. & Goldberg, J.P. (1968). Pure-tone intensity discrimination and energy detection, *Journal of the Acoustical Society of America*, 44, 2, 576-581, ISSN 0001-4966.
- Moore, B.C.J., Glasberg, B.R. & Baer, T. (1997). A model for the prediction of thresholds, loudness, and partial loudness, *Journal of the Audio Engineering Society*, 45, 4, 224-240, ISSN 1549-4950.
- Nizami, L. (2001). A rate-level equation that contains the four quantities reported from experiment, and in the units favored by experimentalists, *Abstracts of the Association for Research in Otolaryngology*, 24, 102.
- Nizami, L. (2002). Estimating auditory neuronal dynamic range using a fitted function, *Hearing Research*, 167, 1-2, 13-27, ISSN 0378-5955.
- Nizami, L. (2003). Afferent response parameters derived from postmasker probe-detection thresholds: „The decay of sensation“ revisited, *Hearing Research*, 175, 1-2, 14-35, ISSN 0378-5955.
- Nizami, L. (2005a). Dynamic range relations for auditory primary afferents, *Hearing Research*, 208, 1-2, 26-46, ISSN 0378-5955.
- Nizami, L. (2005b). Intensity-difference limens predicted from the click-evoked peripheral N_1 : the mid-level hump and its implications for intensity encoding, *Mathematical Biosciences*, 197, 1, 15-34, ISSN 0025-5564.
- Nizami, L. (2009). An important flaw in American National Standards Institute ANSI S3.4-2007 and why it happened, *World Academy of Science, Engineering, and Technology, Proceedings Vol. 55 (International Conference on Mathematical Biology)*, pp. 689-693, ISSN 2070-3724, Oslo, Norway, July 2009, Open Science Research, Oslo, Norway.
- Nizami, L. & Schneider, B.A. (1997). Auditory dynamic range derived from the mean rate-intensity function in the cat, *Mathematical Biosciences*, 141, 1, 1-28, ISSN 0025-5564.
- Ohlemiller, K.K., Echteler, S.M. & Siegel, J.H. (1991). Factors that influence rate-versus-intensity relations in single cochlear nerve fibers of the gerbil, *Journal of the Acoustical Society of America*, 90, 1, 274-287, ISSN 0001-4966.
- Palmer, A.R. & Evans, E.F. (1979). On the peripheral coding of the level of individual frequency components of complex sounds at high sound levels, In: *Hearing Mechanisms And Speech*, O. Creutzfeld, H. Scheich, & Chr. Schreiner (Eds.), pp. 19-26, Springer-Verlag, ISBN 0387096558, Heidelberg, Germany.
- Palmer, A.R. & Evans, E.F. (1980). Cochlear fibre rate-intensity functions: no evidence for basilar membrane nonlinearities, *Hearing Research*, 2, 3-4, 319-326, ISSN 0378-5955.
- Perez, M. & Coro, F. (1985). Physiological characteristics of the tympanic organ in noctuid moths. II. Responses to 45 ms and 5 s acoustic stimuli, *Journal of Comparative Physiology*, 156, 5, 689-696, ISSN 0340-7594.
- Pfeiffer, R.R. & Kim, D.O. (1975). Cochlear nerve fiber responses: distribution along the cochlear partition, *Journal of the Acoustical Society of America*, 58, 4, 867-869, ISSN 0001-4966.
- Plontke, S.K.-R., Lifshitz, J. & Saunders, J.C. (1999). Distribution of rate-intensity function types in chick cochlear nerve after exposure to intense sound, *Brain Research*, 842, 1, 262-274, ISSN 0006-8993.
- Poulton, E.C. (1984). A linear relation between loudness and decibels, *Perception & Psychophysics*, 36, 4, 338-342, ISSN 0031-5117.

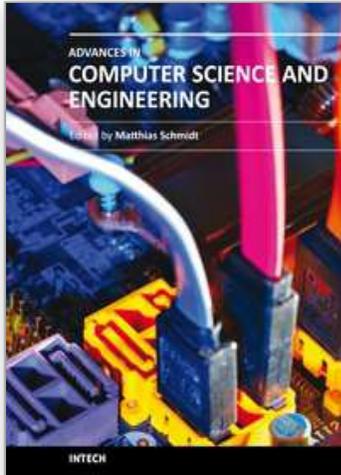
- Raab, D.H. & Goldberg, I.A. (1975). Auditory intensity discrimination with bursts of reproducible noise, *Journal of the Acoustical Society of America*, 57, 2, 437-447, ISSN 0001-4966.
- Richter, C.-P., Heynert, S. & Klinke, R. (1995). Rate-intensity-functions of pigeon auditory primary afferents, *Hearing Research*, 83, 1-2, 19-25, ISSN 0378-5955.
- Sachs, M.B. & Abbas, P.J. (1974). Rate versus level functions for auditory-nerve fibers in cats: tone-burst stimuli, *Journal of the Acoustical Society of America*, 56, 6, 1835-1847, ISSN 0001-4966.
- Sachs, M.B., Winslow, R.L. & Sokolowski, B.H.A. (1989). A computational model for rate-level functions from cat auditory-nerve fibers, *Hearing Research*, 41, 1, 61-70, ISSN 0378-5955.
- Sachs, M.B., Woolf, N.K. & Sinnott, J.M. (1980). Response properties of neurons in the avian auditory system: comparisons with mammalian homologues and consideration of the neural encoding of complex stimuli, In: *Comparative Studies Of Hearing In Vertebrates*, A.N. Popper & R.R. Fay (Eds.), pp. 323-353, Springer-Verlag, ISBN 0387904603, New York, NY, USA.
- Schacknow, P. & Raab, D.R. (1976). Noise-intensity discrimination: effects of bandwidth conditions and mode of masker presentation, *Journal of the Acoustical Society of America*, 60, 4, 893-905, ISSN 0001-4966.
- Schiaffino, P. (1957). Méthodes objectives de mesure de l'équivalent de référence et de l'affaiblissement équivalent de netteté en téléphonométrie, *Annales des Télécommunications*, 12, 10, 349-358, IDS O1223.
- Siebert, W.M. (1965). Some implications of the stochastic behavior of primary auditory neurons, *Kybernetik*, 2, 5, 206-215, ISSN 0023-5946.
- Stevens, S.S. (1956). The direct estimation of sensory magnitudes - loudness, *American Journal of Psychology*, 69, 1, 1-25, ISSN 0002-9556.
- Swets, J.A. (1961). Is there a sensory threshold?, *Science*, 134, 347, 168-177, ISSN 0036-8075.
- Temchin, A.N. & Moushegian, G. (1992). Is avian basilar membrane truly linear?, *Society for Neuroscience Abstracts*, 18, 1190.
- Viemeister, N.F. (1983). Auditory intensity discrimination at high frequencies in the presence of noise, *Science*, 221, 4616, 1206-1208, ISSN 0036-8075.
- Viemeister, N.F. (1988). Intensity coding and the dynamic range problem, *Hearing Research*, 34, 3, 267-274, ISSN 0378-5955.
- Whitfield, I.C. (1967). Coding in the auditory nervous system. *Nature*, 213, 756-760.
- Winslow, R.L. & Sachs, M.B. (1988). Single-tone intensity discrimination based on auditory-nerve rate responses in backgrounds of quiet, noise, and with stimulation of the crossed olivocochlear bundle, *Hearing Research*, 35, 2-3, 165-190, ISSN 0378-5955.
- Winter, I.M., Robertson, D. & Yates, G.K. (1990). Diversity of characteristic frequency rate-intensity functions in guinea pig auditory nerve fibres, *Hearing Research*, 45, 3, 191-202, ISSN 0378-5955.
- Yates, G.K. (1990). Basilar membrane nonlinearity and its influence on auditory nerve rate-intensity functions, *Hearing Research*, 50, 1-2, 145-162, ISSN 0378-5955.
- Yates, G.K., Manley, G.A. & Koppl, C. (2000). Rate-intensity functions in the emu auditory nerve, *Journal of the Acoustical Society of America*, 107, 4, 2143-2154, ISSN 0001-4966.

Yates, G.K., Winter, I.M. & Robertson, D. (1990). Basilar membrane nonlinearity determines auditory nerve rate-intensity functions and cochlear dynamic range, *Hearing Research*, 45, 3, 203-220, ISSN 0378-5955.

Zwislocki, J. J. (1965). Analysis of some auditory characteristics, In: *Handbook of Mathematical Psychology*, Vol. 3, R.D. Luce, R.R. Bush & E. Galanter (Eds.), pp. 1-98, Wiley, ASIN B000RFSIFW, New York, NY, USA.

IntechOpen

IntechOpen



Advances in Computer Science and Engineering

Edited by Dr. Matthias Schmidt

ISBN 978-953-307-173-2

Hard cover, 462 pages

Publisher InTech

Published online 22, March, 2011

Published in print edition March, 2011

The book *Advances in Computer Science and Engineering* constitutes the revised selection of 23 chapters written by scientists and researchers from all over the world. The chapters cover topics in the scientific fields of Applied Computing Techniques, Innovations in Mechanical Engineering, Electrical Engineering and Applications and Advances in Applied Modeling.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

Lance Nizami (2011). Lütkenhöner's „Intensity Dependence of Auditory Responses“: An Instructional Example in How Not To Do Computational Neurobiology, *Advances in Computer Science and Engineering*, Dr. Matthias Schmidt (Ed.), ISBN: 978-953-307-173-2, InTech, Available from: <http://www.intechopen.com/books/advances-in-computer-science-and-engineering/l-tkenh-ner-s-intensity-dependence-of-auditory-responses-an-instructional-example-in-how-not-to-do-c>

INTECH
open science | open minds

InTech Europe

University Campus STeP Ri
Slavka Krautzeka 83/A
51000 Rijeka, Croatia
Phone: +385 (51) 770 447
Fax: +385 (51) 686 166
www.intechopen.com

InTech China

Unit 405, Office Block, Hotel Equatorial Shanghai
No.65, Yan An Road (West), Shanghai, 200040, China
中国上海市延安西路65号上海国际贵都大饭店办公楼405单元
Phone: +86-21-62489820
Fax: +86-21-62489821

© 2011 The Author(s). Licensee IntechOpen. This chapter is distributed under the terms of the [Creative Commons Attribution-NonCommercial-ShareAlike-3.0 License](#), which permits use, distribution and reproduction for non-commercial purposes, provided the original is properly cited and derivative works building on this content are distributed under the same license.

IntechOpen

IntechOpen