

## Comments

### Comment by Kohlrausch:

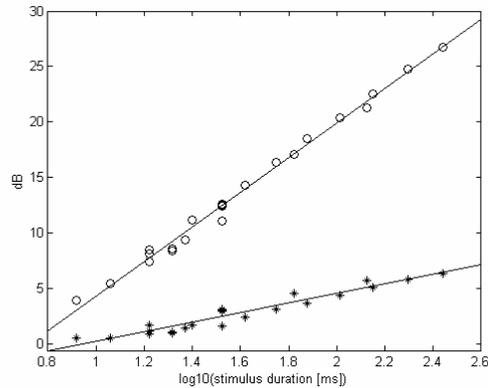
This comment focuses on the analysis of the perceptual data, in particular human, and does not address any of the physiological aspects (timing of the first spike). The summary of my comment is as follows: The analysis does not support the claim that “integration of  $P(t)$  provides a much better explanation for threshold than that of  $I(t)$ ”.

1) Statistical argument: Comparison of correlation coefficients (or, alternatively, the variance not explained by linear regression) is inappropriate for comparison of quality of fit for data sets with largely different ranges of the dependent values. The interesting quantity to compare is the goodness of fit, which can, e.g., be computed by the sum of the squared deviations from the regression curve, *once the dependent variables of the two data sets are expressed in a comparable way*. For behavioral data, in which the threshold quantity is expressed in dB SPL, the dependent variable should therefore be expressed on an appropriate dB scale.

2) Data representation in Fig. 1c and d: These two panels suggest that there is a much larger variability (deviation from linear relation) in panel c (intensity integral) than in panel d (pressure integral). However, the ordinate scales differ strongly. The ordinate in panel d covers a slightly greater range relative to the quantities than panel c. More importantly, both are linear, ignoring the fact that the quantity in panel c is quadratic (integration of intensity) while the one in panel d is linear (pressure). If values are first transformed to a dB scale and plotted with the same resolution, the deviation from linear regression is comparable for the two representations (see Fig. A1 below).

I start with the graphic representation, because this will help to understand the statistical argument. I recalculated from the original mean data from Gerken *et al.* the pressure and intensity integrals (which, in the limits of visual accuracy, agree well with the values published in the conference paper and in the PNAS publication). I then transformed their values to dB, by computing  $20\log(P_t)$  and  $10\log(I_t)$  (the index  $t$  indicates integration over time as in the article). The two data sets are plotted as a function of  $\log(\text{stimulus duration})$  in Fig. A1, with linear regression lines.

The data marked with circles ( $\circ$ ) correspond to the points in panel 1d of Heil and Neubauer (human data, use right axis in that figure to compare linear values with dB values shown here), the data marked as stars (\*) to the points in panel 1c. Please note that, in order to fit the curves into the same figure, I expressed the intensity values as  $[\text{pWsm}^{-2}]$ , while Heil and Neubauer used  $[\text{fWsm}^{-2}]$ , thus my numerical values are a factor 1000 smaller than theirs. In Fig. A1, deviations in dB between each data set and the corresponding the regression line are approximately equally large, in contrast to what one concludes from looking at the figure in the conference and the PNAS papers.



**Fig. A1:** Pressure ( $\circ$ ) and intensity integrals ( $*$ ), expressed in dB, of data from Gerken *et al.* (1990) as a function of  $\log(\text{stimulus duration})$ .

Moving on to point 1, the statistical argument: The authors argue that the pressure envelope integration thresholds are an excellent fit, because this analysis leaves only 0.84% unexplained variance (for the human data). In contrast, the intensity integral leaves 10.8% unexplained, an order of magnitude larger. I don't argue about these values, in my own analysis of these data, the values were 0.78 and 7.4%, respectively.

My point is that the correlation measure isn't appropriate to compare the goodness of fits. The correlation measure is influenced by two quantities: on the one hand, the covariance, which is a measure for the deviation from linearity of the relation between independent and dependent variables, and on the other hand a term characterizing the overall variability of the dependent variable (and the independent variable, but we can ignore this, because the range of durations is the same for both derived quantities). For the computation of the Pearson moment correlation coefficient (the  $r$ ), these two values are divided one by the other. Thus, *only if the sets of dependent variables have the same overall variance*, the correlation value is a direct measure for the deviation from a linear relation. In the present case, pressure varies much more with duration (leading to a greater variance) than intensity. Variability in the pressure data is dominated by the overall trend (15 dB increase per decade of duration), and hardly affected by the deviation from the linear regression curve (limited to maximally 1.5 dB per data point), leading to a high  $r$ , while in the intensity data, the slope is only 4 dB/decade and thus the random variability contributes much more. The correlation coefficient indicates the reduction in variance by a linear relation between independent and dependent variable, *compared to having no model*, and therefore will be higher in the first case.

Two extreme cases: If the integrated quantity (e.g., intensity) at threshold was *independent of duration*, a linear regression analysis (of real data which always contain a small random fluctuation around this constant value) would not explain *any* of the variance, and the correlation would be close to zero. At the other extreme, if we analyzed the present data set by integrating the *square root* of the

pressure (which would add approximately an extra 10 dB/decade to the slope of the data), the unexplained variance would decrease even further and the correlation coefficient would increase.

A more appropriate measure of quality in the present case is the quadratic deviation of predicted from measured values, e.g. the total squared error. For the 24 data points I analyzed (the conditions from Gerken *et al.* also analyzed by Heil and Neubauer), this value is 6.9 dB for pressure and 5.2 dB for intensity. Thus, in line with the graphical representation in Fig. A1, there is no indication of a better fit of the data using the pressure integral.

Finally, whether pressure or intensity is integrated can best be distinguished if stimuli with the same overall duration but very different envelope structures are compared, like the multiple-burst and the single-burst stimuli of Gerken *et al.* (1990). I so far found only one data set which fulfills this criterion (Booth and Cramb, *Hear. Res.* 52 (1991), 312-320: Threshold integration of bi-amplitude signals). These authors measured absolute thresholds for 1000-Hz sinusoids of total duration 100 ms. The waveform was portioned into two segments, with durations of 25 ms and 75 ms, with 10 ms raised cosine on/off ramps and transition. The level of the longer segment was lower than the shorter by one of the following values: 15, 10, 5, 3, 2, 1 or 0 dB (the last stimulus is, *de facto*, a 100-ms stimulus). For each stimulus I computed the integral of both the pressure envelope and the intensity. Expressed in dB, the range of values was 2.9 dB with a standard deviation of 1.0 dB for pressure, and 1.0 dB with a standard deviation of 0.38 dB for intensity. In this example the intensity integral leads to a more constant value than the pressure integral.

## Reply

We re-emphasize that our claim is based on the obviously closer alignment of thresholds for stimuli of the different series tested by Gerken *et al.* (1990), viz., single burst, multiple burst, onset-offset and interval series, when thresholds are expressed in terms of integrated  $P(t)$  compared to integrated  $I(t)$  (see Fig. 1 of our chapter, and Heil & Neubauer, *Proc. Natl. Acad. Sci. USA* 100: 6151-6156, 2003, p. 6154, left column bottom). Below we will present an additional analysis which quantifies the alignment objectively and strongly supports our claim.

Kohlrausch focusses his critique on the fact that we use differences in Pearson's correlation coefficient  $r$ , or in  $1-r^2$  as the variance unexplained, for linear regressions of the thresholds expressed in pressure or intensity and plotted against stimulus duration, in log-log coordinates, as an additional indication for the superiority of one over the other model. He argues that  $r$  is inappropriate to compare the quality of fits for different data sets with largely different ranges of the dependent values. However, this argument is not of general validity.  $r$  is invariant with respect to changes of axis scaling, of the position of the origin (e.g. Voß, *Taschenbuch der Statistik*, Carl Hanser, 2000, p. 188), and of the choice of the physical units of the dependent and/or independent variables. When logarithmic values of a variable are used to compute the correlation, as in our case (note that the linear threshold values are plotted on logarithmically scaled axes in Fig. 1c,d),  $r$  is also unaffected by a change of the exponent of the argument of the logarithm. In

our case, the arguments of the logarithms of the two threshold measures do not simply differ in their exponents, although  $I(t) \propto P(t)^2$ , since these terms are integrated over time. It is the integration and thus the influence of the integration variable which compromises the invariance of  $r$  somewhat, and not the squaring operation, as Kohlrausch seems to suggest. Nevertheless, as will be shown below,  $r$  remains sensitive enough to distinguish between the two models. Kohlrausch is correct that the use of  $r$  is inappropriate in the extreme case of independence, but this does not apply here: the logarithms of both threshold measures increase significantly with increasing logarithm of the stimulus duration (Kendall's  $\tau=0.942$ ;  $p=1.1E-10$  for integrated  $P(t)$ , and  $\tau=0.807$ ;  $p=3.2E-8$  for integrated  $I(t)$ ).

Kohlrausch suggests to use, instead of  $r$ , the sum of squared deviations from a regression line as a measure of the goodness of fit of the two models. This measure requires that the deviations of the data from the regression lines are expressed in a comparable way and the differences between the competing models are maintained. Kohlrausch's suggestion to transform the thresholds, expressed either in [Pa s] or in [W s m<sup>-2</sup>], into a seemingly common dB-scale appears, at first sight, to achieve the comparability. But this comes at the cost of substantially distorting the differences that are essential to distinguish between the models. This distorting effect results from applying the inverse function of that function which actually generates the differences between the models. Specifically, Kohlrausch's procedure is equivalent to comparing the square root of the integral of a squared quantity to the integral of the quantity itself. The square-root operation is implemented by taking factors of 20 and 10 for the logarithms of thresholds expressed in terms of integrated  $P(t)$  or  $I(t)$ , respectively, as is, for example, easily seen for a stimulus of rectangular  $P(t)$ , for which:  $10 \cdot \log(P(t)^2 \cdot t) = 20 \cdot \log(P(t) \cdot t^{0.5})$ . Thus, Kohlrausch's result of similar sums of squared deviations for the two threshold models may not be too surprising, because the formulae for calculating dBs are designed to return identical values for pressure and intensity for stationary signals.

This is not obvious from the figure of Kohlrausch, because he uses arbitrary and time-independent references, viz. the physical units of integrated pressure envelope ( $\mu\text{Pa s}$ ) and of energy density ( $\text{pW s m}^{-2}$ ), and then multiplies the logarithms of the resulting numbers by 20 and 10, respectively, to calculate dB-values (for convenience referred to as  $\text{dB}_K$ ). But it does become obvious when one uses the defined values in acoustics, viz. 20  $\mu\text{Pa}$  for pressure and 0.966184  $\text{pW m}^{-2}$  for intensity (given a specific impedance of 414  $\text{Pa s m}^{-1}$ ), and time-dependent references generated by multiplying these values with the appropriate stimulus duration. This procedure leads to dB-values (for convenience termed  $\text{dB}_{\text{HN}}$ ) which correspond to the mean amplitude and mean intensity of the stimuli during their duration. These values yield a picture different from that shown by Kohlrausch (cf. Fig. A2a,b). Now the thresholds, in  $\text{dB}_{\text{HN}}$ , for the two competing models are similar and for long-duration tones nearly identical, exactly as expected. The sums of the squared deviations (in  $\text{dB}_{\text{HN}}^2$  or  $\text{dB}_K^2$ ) from the regression lines are unaffected by the choice of the reference.

With changes in the exponent  $q$  of  $P(t)$  within the integrand, thresholds (in  $\text{dB}_{\text{HN}}$  or  $\text{dB}_K$ ; where the factor before the logarithm equals  $20/q$ ) for the single burst series (i.e. the stimuli with plateau) shift relative to those for stimuli without plateau

(Fig. A2a,b). For  $q=1$ , thresholds for the single-burst series (filled circles) are slightly above those of the multiple-burst series (open circles), whereas for  $q=2$  the situation is reversed. For  $q=1.22$ , there is a rather close alignment of the data points for these two series (for clarity only shown in Fig. A2a). Consequently, with changes in  $q$  the sum of the squared deviations (in  $\text{dB}_{\text{HN}}^2$  or  $\text{dB}_{\text{K}}^2$ ) also varies. When thresholds to all stimuli are considered, this measure reaches a minimum at  $q=1.41$  (Fig. A2c; filled diamonds), and when thresholds to only the single- and multiple-burst series are considered a minimum at  $q=1.36$  (Fig. A2c; filled squares). Thus, despite the fact that the definitions of  $\text{dB}_{\text{K}}$ - or  $\text{dB}_{\text{HN}}$ -values tend to distort differences between the models, minima do occur and notably at values of  $q$  closer to 1 than to 2. The relatively large deviations from  $q=1$  are partly due to the variable factor  $20/q$  used to calculate these dB-values. If that factor is held constant (the resultant values will be termed  $\text{dB}_{\text{CF}}$ -values), the minimum shifts to  $q=1.23$  in the latter case (Fig. A2c; open squares), while in the former case the minimum is lost but a shoulder (i.e., a minimum of the first derivative of the function) is retained around  $q=1$  (Fig. A2c; open diamonds). In both cases, the sums of the squared deviations (in  $\text{dB}_{\text{CF}}^2$ ) are considerably larger for  $q=2$  than for  $q=1$ .

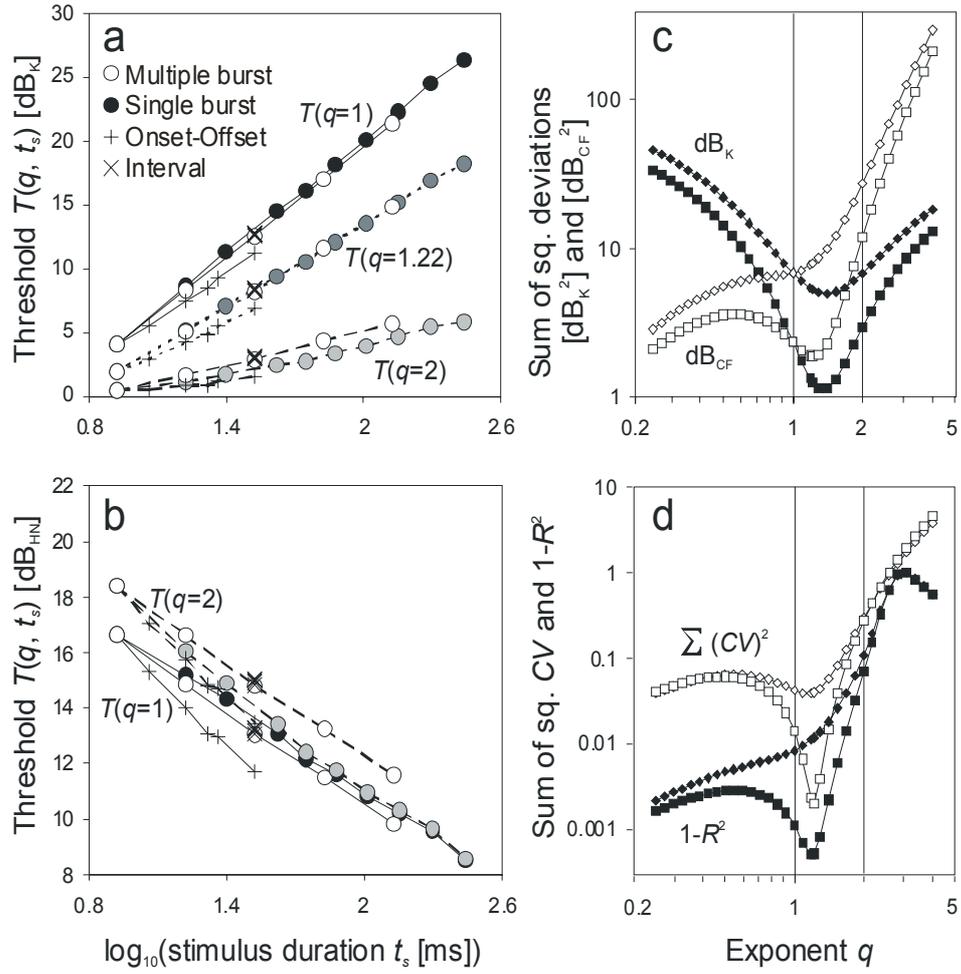
Remarkably, the unexplained variance,  $1-r^2$ , shows a dependence on the exponent  $q$  (Fig. A2d; filled squares and diamonds) very similar to the sum of the squared deviations of  $\text{dB}_{\text{CF}}$ -values (cf. Fig. A2c,d; the minimum is reached at  $q=1.19$ ). As predicted by Kohlrausch,  $1-r^2$  has the general tendency to decrease with decreasing  $q$ . This is so because any quantity raised to some power  $q$  will approach 1 as  $q$  approaches zero. This tendency can obscure the minimum, which would identify the optimal model. This seems to be the case here when thresholds to all stimuli are included, but not when only thresholds to the single- and multiple-burst series are considered (Fig. A2d; filled diamonds and filled squares). Still, all measures of distance from a regression line discussed so far, viz., the sum of squared deviations (whether expressed in  $\text{dB}_{\text{K}}^2$ ,  $\text{dB}_{\text{HN}}^2$ , or in  $\text{dB}_{\text{CF}}^2$ ) and  $1-R^2$ , reveal minima or shoulders at values of  $q$  closer to 1 than to 2.

To critically test the optimum value of  $q$ , we finally introduce a measure of distance from perfect alignment of thresholds at any given duration, which is independent of a specific assumption about the dependence of thresholds on stimulus duration (e.g. a power law) and which ensures a maximum degree of comparability between the competing models. This measure of distance is the summed squared coefficient of variation,  $\Sigma(CV)^2$ , and was calculated as follows. For a given stimulus duration and for a given  $q$ , we first calculated the coefficient of variation,  $CV$ , defined as the ratio of the square root of the mean squared deviations to the mean threshold across the series. In this way, the standard deviation is normalized by the mean threshold at every stimulus duration.  $CV$  operates on the ratio level and thus requires to take the linear values of the thresholds.  $CV$  was calculated for all durations for which thresholds from at least two series were actually available or one was available and at least one other could be obtained via linear interpolation on double-log axes. In this way, a range of durations from 11.52 to 133.12 ms could be evaluated. The coefficients were then squared and summed across all durations to yield  $\Sigma(CV)^2$ . Functions relating  $\Sigma(CV)^2$  to the exponent  $q$  are shown in Fig. A2d for all stimuli (open diamonds) and for those of the single- and

multiple-burst series only (open squares). Both functions exhibit clear minima, i.e. alignment is best, at values of  $q=1.15$  and  $q=1.22$ , respectively, i.e. close to 1, and  $\Sigma(CV)^2$  is much larger for  $q=2$  than for  $q=1$  (by factors of 4.3 and 5.1, respectively). Furthermore, note that the overall shapes of these functions are very similar to those of  $I-r^2$  (cf. open with filled symbols in Fig. A2d), supporting the usefulness of  $I-r^2$  to distinguish between the models. Overall, the minima and shoulders found in all these functions correspond closely to the situation of best alignment of thresholds for the single- and multiple-burst series. These results thus corroborate the validity of our previous conclusion that integration of  $P(t)$  provides a better description of thresholds than integration of  $I(t)$ .

Kohlrausch is correct in that stimuli of different shape are needed to distinguish between the models, such as the data of Gerken et al. (1990) and Solecki and Gerken (1990). And, the study of Booth and Cramb (*Hearing Res.* 52: 312-320, 1991), referred to by Kohlrausch, appears to be currently the only other one which contains data of use for the issue. We have therefore also re-analyzed these data using  $\Sigma(CV)^2$  as the measure of distance. Figure 3 of Booth and Cramb (1991) shows mean thresholds (in dB SPL) for bi-amplitude signals with amplitude ratios of 1,2,3,5 and 10 dB where the short, higher-amplitude segment precedes the long, lower-amplitude segment as well as for the temporally reversed stimuli. Together with the mean threshold for the 100-ms tone of constant plateau amplitude, obtained from the same group of subjects and illustrated in Fig. 2 of Booth and Cramb (1991), thresholds to 11 signals, all of 100 ms total duration, were obtained.  $\Sigma(CV)^2$  for these thresholds did not yield a minimum at a particular value of  $q$ , unlike the functions obtained from the Gerken et al. (1990) data (Fig. A2d), but a shoulder at  $q=1.18$  (not shown). A similar value, viz.  $q=1.14$ , was obtained from the same analysis applied to the thresholds averaged across the two temporally reversed stimuli, and as shown in Fig. 4 of Booth and Cramb (1991). The 6 values (in dB SPL) which we used for this analysis were identical to those used by Kohlrausch. We only omitted the one for the 15-dB bi-amplitude signal shown there, because Booth and Cramb (1991) obtained this threshold from a different group of subjects with a different mean sensitivity.

In summary then, these novel analyses of the human perceptual data of Gerken et al. (1990) strongly favor a model for thresholds based on temporal integration of  $P(t)$  over one based on temporal integration of  $I(t)$  and the data by Booth and Cramb (1991) are consistent with this.



**Fig. A2:** **a.** Thresholds  $T(q, t_s)$  from Gerken et al. (1990), expressed in dB<sub>K</sub> as explained in the text, and plotted against  $\log(\text{stimulus duration } t_s \text{ [ms]})$  for  $q=1$ ,  $q=1.22$ , and  $q=2$ . **b.** Same data, expressed in dB<sub>HN</sub> as explained in the text, and plotted against  $\log(\text{stimulus duration } t_s \text{ [ms]})$  for  $q=1$  and  $q=2$ . **c.** Sum of squared deviations from a linear regression between log threshold and log stimulus duration and plotted as a function of the exponent  $q$  of  $P(t)$ . The measure is calculated for all stimuli (diamonds) or for stimuli of the single- and multiple-burst series only (squares), and expressed in dB<sub>K</sub><sup>2</sup> (filled symbols) or dB<sub>CF</sub><sup>2</sup> (open symbols). **d.** The variance unexplained ( $1-R^2$ ) by the linear regression between log threshold and log stimulus duration (filled symbols) and  $\Sigma(CV)^2$  (open symbols) are plotted as a function of  $q$ . The measures are shown for all stimuli (diamonds) or for stimuli of the single- and multiple-burst series only (squares).

### Comment by Lutkenhöner:

In view of the high complexity and the numerous non-linearities of the auditory system it is surprising that a great variety of data could be explained so nicely by simple models based on the integration of pressure envelope raised to some power,  $q$ . However, this great success does not ensure that the model parameters have a simple physiological interpretation. Thus, focusing on the question as to whether the data are better explained by assuming  $q=1$  (pressure envelope integration) or  $q=2$  (energy integration) might not get us any further. For the perceptual data (Fig. 1c-d), both types of integration result in a threshold linearly increasing with stimulus duration (on double log scales). Compared to this main effect, the choice of  $q$  appears to be of secondary importance. A different situation can be observed in Fig. 1c of Heil and Neubauer (2003), showing data from an exemplary AI neuron: While threshold derived by pressure envelope integration exhibits a roughly linear increase with the logarithm of integration time, threshold derived by energy integration appears to be roughly constant (supposed that we are willing to ignore the considerable scatter). This would mean that the assumption of energy integration resulted in the simpler model so that it might be tolerable that the scatter of the derived thresholds is apparently larger than for pressure envelope integration. It appears worth mentioning in this context that the scatter of the thresholds derived for energy integration would be considerably reduced if “threshold” would be defined in terms of the square root of the integrated energy (*de facto* resulting in a quantity being comparable to the integrated pressure envelope).

Irrespective of the above reservation, the assumption of pressure envelope integration seems to be more plausible than the assumption of energy integration, because a reconciliation of the latter assumption with the limited dynamic range of single neurons and the compressive properties of the auditory system appears difficult. The article by Heil and Neubauer provides good arguments for the hypothesis that the integrator is not leaky. But how does the integrator “know” when to start the integration? This may not be a problem for a stimulus presented in absolute silence, because integration could start long before the actual onset of the stimulus. However, this is not the typical situation in natural environments. Evolution probably optimized the auditory system for the detection of weak relevant sounds embedded in an irrelevant background. It is hardly conceivable that this task can be solved by a mechanism lacking the ability to forget. A conceivable solution might be that, in some respect, higher auditory processing compensates for leaky integration taking place in earlier processing stages.

Heil, P. and Neubauer, H. (2003). Proc. Nat. Acad. Sci. USA 100, 6151-6156.

### Reply

Lütkenhöner points to a main effect, viz. that perceptual thresholds, expressed as the temporal integral of  $P(t)^q$  increase with stimulus duration according to a power law, regardless of whether  $q=1$  or  $q=2$ , and argues that, compared to this effect, the choice of  $q$  appears of secondary importance. As is evident from the comment of Armin Kohlrausch and from our reply to his comment, the correct  $q$  is of

considerable interest and significance. As detailed there, we remain convinced that  $q=1$  yields a better model than  $q=2$ .

Lütkenhöner draws attention to Fig. 1c of our publication in PNAS (Heil and Neubauer, 2003) which shows data from an exemplary primary auditory cortical neuron. He points out that this neuron's thresholds when expressed in terms of integrated  $P(t)$ , i.e.  $q=1$ , increase with integration time, but when expressed in terms of integrated  $I(t)$ , i.e.  $q=2$ , appear to be roughly constant. Thus, if one were willing to ignore the considerable vertical scatter of thresholds in the latter case, integration of  $I(t)$  appears to be the simpler model. Three points must be made here:

1) We are not willing to ignore the vertical scatter of thresholds. In fact, we used it as one criterion to find the optimal  $q$  and this scatter is considerably smaller for  $q=1$  than for  $q=2$ . As explained in our response to Kohlrausch, taking the square root of integrated  $I(t)$  does not result in a quantity comparable to the integrated  $P(t)$ .

2) With increasing  $q$ , the only free parameter in the fits, viz. the estimated minimum latency  $L_{min}$  (interpretable as a transmission delay), also increases. This has the consequence that for  $q=2$ ,  $L_{min}$  is longer than about 20% of mean latencies recorded from this neuron (in response to high-SPL, short-rise time tones). Thus, these responses are unexplained by the threshold model based on integration of  $I(t)$ ! The percentage of unexplained responses is zero for the threshold model based on integration of  $P(t)$ . Both issues are discussed in the PNAS-paper.

3) The threshold of the exemplary neuron when expressed in terms of integrated  $I(t)$  is not really constant, it just does not vary monotonically with integration time. A constancy of such thresholds would also be at variance with the time-dependence of equivalently defined perceptual thresholds. We agree with Lütkenhöner's proposition that a threshold which appears roughly independent of integration time constitutes the simpler, and hence better, model. We come close to such a constant threshold by the formulation of the final equation in the chapter and PNAS-paper:

$$\overline{R} \cdot t_s = const.$$

Thresholds, as they are currently defined, are not independent of time. To remind the reader: the amplitude of  $P(t)$ , and hence also of  $I(t)$ , at which threshold is reached decreases as the time needed to reach threshold increases (e.g. Heil & Irvine, *NeuroReport* 7: 3073-3076, 1996; Heil, *J. Neurophysiol.* 77: 2616-2641, 1997; Heil & Irvine, *Cerebral Cortex* 8: 125-141, 1998; Biermann & Heil, *J. Neurophysiol.* 84: 2426-2439, 2000; Heil & Neubauer, *J. Neurosci.* 21:7404-7415, 2001; Heil & Neubauer, *Proc. Natl. Acad. Sci. USA* 100:6151-6156, 2003). The psychoacoustic studies show much of the same: threshold SPL decreases as stimulus duration increases. Conversely, thresholds expressed in terms of integrated  $P(t)$  or integrated  $I(t)$  both increase with duration (see Fig. 1c,d). Intracellular recordings from cortical neurons (see e.g. Fig. 4.3. in Creutzfeld, *Cortex Cerebri*, Oxford University Press, 1995) show that, in response to ramp-like current injections, spike threshold is reached at a current which systematically decreases as the slope of the ramp decreases and the time needed to reach threshold increases (much like what is observed for the amplitude of  $P(t)$  at which the first spike of auditory neurons is triggered or perceptual thresholds are reached). The injected current integrated over time yields charge, and the total charge needed for the neuron to reach threshold increases with the time needed to reach threshold (much

like the integrated  $P(t)$  or  $I(t)$  in the auditory case). Similar results have been published for octopus cells from the mammalian ventral cochlear nucleus (Ferragamo & Oertel, *J. Neurophysiol.* 87: 2262-2270, 2002). This study also shows that the membrane potential at which the first spike is triggered is also not constant. Rather, spike generation depends on the rate of rise of the membrane potential as well, a fact also noted by others (Ebbinghaus, Diesmann, Rotter & Aertsen, *Proc. Göttingen Neurobiol Conf.*, Thieme, 1997; Naundorf, Wolf & Volgushev, *Proc. Göttingen Neurobiol Conf.*, Thieme, 2003). Taken together, thresholds being reached by surpassing a fixed pressure, pressure integral, energy, current, charge, or voltage may be conceptionally simple, but in nature appear to be the exception rather than the rule.

Lütkenhöner also raises the issue of how the integrator, proposed by us, could deal with suprathreshold stimuli, e.g. how it “knows” when to start integrating and how it “forgets”. These are interesting questions, but go far beyond the scope of our papers under discussion here.