Hearing Research, 21 (1986) 195–204
Elsevier

HRR 00689

The influence of cochlear hearing loss and probe tone level on compound action potential tuning curves in humans *

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(Received 29 July 1985; accepted 1 December 1985)

The effect of cochlear hearing loss and of probe tone level on slopes and sharpness of compound action potential tuning curves was investigated. Thirty-one simultaneously masked isoreduction (50%) tuning curves were determined in 26 adults with cochlear hearing losses up to 60 dB. Probe tone frequency was 2 or 3 kHz. Probe tone level was chosen as close as possible to the action potential threshold, usually within 30 dB. In 5 cases a second tuning curve was determined at a 20–30 dB higher probe tone level in order to differentiate between effects of hearing loss and of probe tone level itself on decrease of selectivity. Tuning was analysed in terms of high- and low-frequency slopes of the tuning curves, both in the steepest parts near the tip and overall, and in terms of Q_{10dB}. Slopes and tuning quality diminished with increasing hearing loss up to 60 dB. Part of the decrease in Q_{10} could be attributed to increased probe tone level, implying that frequency selectivity is also a level-dependent property. In the same group of subjects so called 'narrow-band' (or 'derived response') compound action potential latencies were determined at 90 dB pe SPL and a derived frequency similar to the probe tone in the tuning curve experiments. Narrow band latencies did not change significantly out of the normal range (2 periods) with increasing hearing loss. This implies that narrow band latencies are not related to hearing loss, but reflect only the probe-level dependent impulse response delay. Analysis shows that it is possible to derived Q_{10dB} from narrow band latencies with probe level as a parameter.

compound action potential, tuning, frequency selectivity, derived responses, cochlear pathology, hearing loss

Introduction

Since the introduction and validity proof of compound action potential tuning curves (APTCs) by Dallos and Cheatham (1976) other researchers have described the use, significance and properties of APTCs in animals and humans, both under normal and pathological cochlear conditions.

In animal studies, Harris (1979, chinchilla) showed that APTCs usually are broader than single fibre tuning curves at the same characteristic frequency. This also was shown by Van Heusden and Smoorenburg (1981, cat). Furthermore, they concluded that after noise trauma the APTC broadens and that the use of a higher probe tone level was only partially responsible for this widening. Gorga and Abbas (1981, cat) observed that sharpness of APTCs, expressed in Q_{10dB}, was unaffected by acoustic trauma or probe level, while the low-frequency tail could have become relatively hypersensitive. Shepard and Abbas (1983, cat) correlated APTC findings to histological data of acoustically traumatized ears. They concluded that traumatized ears had a decreased sharpness of tuning and a less sensitive tip and tail region. Also, normal tuning could sometimes go along with hair cell damage. Inner hair cell damage affected the tail position, outer hair cell damage the tip region.

In man, Eggermont (1977) observed broader APTCs in pathological ears with losses over 40 dB. Harrison et al. (1981) quantified Q_{10dB} to be from 2.3 at 2 kHz to 4.7 at 8 kHz in normals and between about 1–2 at 2 kHz and 2.3–4.7 at 8 kHz in case of losses over 40 dB. Rutten and Kuper (1982) investigated Q_{10dB} at a probe frequency of 2 kHz as a function of AP threshold at 2 kHz. A

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good correlation (in a rather limited number of subjects) was found, ranging from $Q_{10dB} = 8$ in normals to $Q_{10dB} \approx 0$ at 60 dB hearing loss.

Given this good correlation in a limited group it was important to enlarge the population in order to establish the relationship more firmly and also to study other measures such as the low- and high-frequency slopes of the APTC, both in the steepest part near the tip and over the entire frequency range. As the work of Møller (1983) indicated that Q_{10dB} diminished as a function of increasing probe tone level, another point of interest was to investigate the effect of probe tone level increase on Q_{10dB} in the same subject.

As each data point of an APTC is the 50% reduction level in a plot of masker level versus probe tone amplitude (usually three to four points) registration of tuning curves is rather time consuming, which is disadvantageous under clinical circumstances. A faster method, yielding information about cochlear frequency selectivity would be of value. Response delay time provides such a possibility, as in a linear filter model filter sharpness is related to response delay (Duifhuis, 1973; Eggermont, 1979; Goldstein et al., 1971; Weiss, 1966). The sharper the filter, the longer is its impulse response group delay. Therefore, in the same group of subjects we measured, besides tuning curves, also the much faster to obtain so-called narrow-band AP latencies (Eggermont, 1979; Evans and Elberling, 1982) in response to click stimuli. We subsequently related both measures to AP thresholds.

Resuming, in this study we focus on two questions. Firstly, is AP frequency selectivity correlated to AP threshold, to probe tone level or to both? Secondly, is narrow-band AP latency correlated to AP threshold? Positive answers with respect to the relations to thresholds could imply a justification of the use of a linear filter model and at the same time also yield a clinically more feasible test for frequency selectivity.

Methods

AP thresholds and AP tuning curves in response to tone burst stimuli and narrow-band APs (NAPs) in response to click stimuli were determined during combined transtympanic electrocochleography (ECoG)/surface brainstem electric response (BER) test procedures (see also Rutten and Kuper (1982)).

Recordings were made in a sound-treated room, stimuli were delivered free-field by a Vitavox GP1 pressure unit, attached to a circular exponential horn (Vitavox, type 190). Distance between entrance to the ear canal and pressure unit was 1.2 m. The response was amplified 20000–50000 times, band pass filtered between 10 Hz and 3 kHz (slopes 12 dB/octave, PAR 129) and averaged 512 times by a DATALAB 4000 system. Analysis time was 15 ms (including 3.5 ms prestimulus time), sampling rate was 16.66 kHz. Averaged responses were stored on flexible discs in a DEC PDP 11/03 minicomputer system for computer-aided read-out and further analysis.

Stimuli for threshold determination were short tonebursts at 0.5, 1, 2, 3, 4 and 8 kHz with trapezoidal envelopes (two periods rise and fall times, 4 ms plateau). Stimulation rate was 8/s. Amplitude and latency of the N_1 wave were determined as a function of stimulus level in 5–10 dB steps between 90 or 100 dB HL and threshold. AP threshold corresponded to a N_1 amplitude of 0.1 μV. AP tuning curves (APTCs) were determined for probe tone bursts of 2 or 3 kHz, at a level of 10–30 dB above AP threshold. A continuous sinusoidal masker tone was applied at levels such that a reduction of 50% of the probe tone response amplitude was obtained. Usually, four masker levels for each masker frequency were sufficient to construct this 50% reduction level by interpolation. Masker frequencies were varied between about 500 Hz and 10 kHz in approximately half-octave steps, except in the vicinity of the tip frequency where steps of 250 Hz were chosen. Masker levels ran up to 100 dB SPL as a maximum. In 6 additional cases a second iso-masking tuning curve was obtained at a 20–30 dB higher test tone level.

NAPs were derived for 90 dB pe SPL, 70 μs rectangular clicks using a simultaneous high pass masking/subtraction paradigm (Eggermont, 1979; Prijs and Rutten, 1982). First, the wide band noise level was adjusted, which just totally masked the click response. Then, at successive cut-off frequencies (10, 8, 6, 4, 3, 2, 1.5, 1, 0.5 kHz) of the high pass filter (slope 96 dB/octave) the masked re-

sponses to the click were determined. Latencies of the difference responses (10–8, 8–6, 6–4 kHz and so on) yielded 'derived' NAP latencies representing the response from approximately successive half-octave-wide cochlear regions.

Subjects

Twenty-six subjects were positioned in a supine position and sedated with 100 mg Nembutal, 25 mg Pethidine and 25 mg Phenergan. All experiments were performed during ECoG/BER examinations. Recording sessions took 2–3 h. Electroaudiometry was the final investigation in the audiometric test battery. All subjects also were extensively analysed by pure tone audiometry, speech audiometry, Alternate Binaural Loudness Balance test, tone decay test and stapedius reflex-threshold and -decay test. Also, vestibular function was examined and X-ray petrosum photographs were taken.

None of the patients showed findings of retrocochlear hearing loss. In one patient, the hearing loss was of mixed conductive/cochlear nature (in the following there has been a correction for this 20 dB conduction loss in this one patient). Recruitment in the ABLB test and abnormally steep N_1-amplitude-versus-input stimulus level curves (input/output curves) was the most common finding. In 5 subjects the hearing loss had started suddenly, at most 6 months before examination. Twelve subjects showed the triad of clinical symptoms of the Ménière syndrome.

AP threshold and pure tone subjective thresholds differed always at most by 15 dB (with a mean difference of 0 dB). As much as possible, subjects were selected on flatness of their audiograms, especially in the frequency region of the tuning curve probe-tone, i.e., 2 or 3 kHz. However, in 7 subjects hearing losses increased by more than 20 dB/octave towards higher frequencies above the probe frequency. In one case this increase was towards lower frequencies below the probe tone.

AP thresholds at the frequency of the tip of the APTC were at most 65 dB. Two subjects fell in the category less than 15 dB, 5 in the range 15–25 dB, 8 in the range 25–35 dB, 4 in the range 35–45 dB, 2 in the range 45–55 dB and 5 in the range 55–65 dB.

Results

Fig. 1 shows an example of an APTC in a subject in the 25–35 dB hearing loss group.

Probe tone burst (+) is chosen at 3 kHz/45 dB HL (corresponding to 50 dB SPL). The masker level at which the probe response was reduced by 50% is denoted by (●). Dashed lines indicate the way straight line two-segment approximations were taken to calculate slopes near the tip of the APTC (s) as well as 'overall' (o). Also sketched are the AP thresholds, the vertical scale should now be read as dB SPL of the test tone.

Figs. 2, 3 and 4 summarize low-level (i.e., probe level ≤ 30 dB above threshold) APTCs across subjects in the five hearing loss categories. For better comparison the abscissa has been normalized to f/f_{probe}. Such a pooling of 13 APTCs ($f_{probe} = 2$ kHz) and 13 APTCs ($f_{probe} = 3$ kHz) is allowed in view of the relatively small difference between Q_{10dB} values of APTCs at these frequencies (Harrison et al., 1981).

A widening of the tuning curve going to higher hearing losses is observed clearly, although within one hearing loss group variability is considerable. Also note that tip and probe frequency do not coincide in all cases.

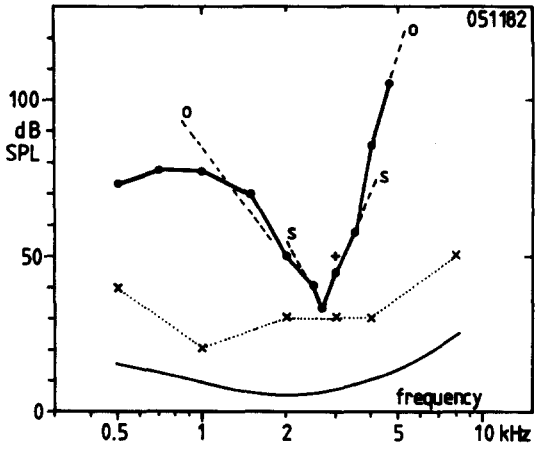

Fig. 1. Example of a compound action potential tuning curve (APTC). Probe tone is indicated by +. Filled circles are masker-levels and -frequencies which reduce the probe tone response (N_1-amplitude) by 50%. Dashed lines are straight-segment approximations near the tip (s) and overall (o). × (dotted curve) are AP-thresholds. Normal AP-thresholds are indicated by the smoothly curved drawn line.

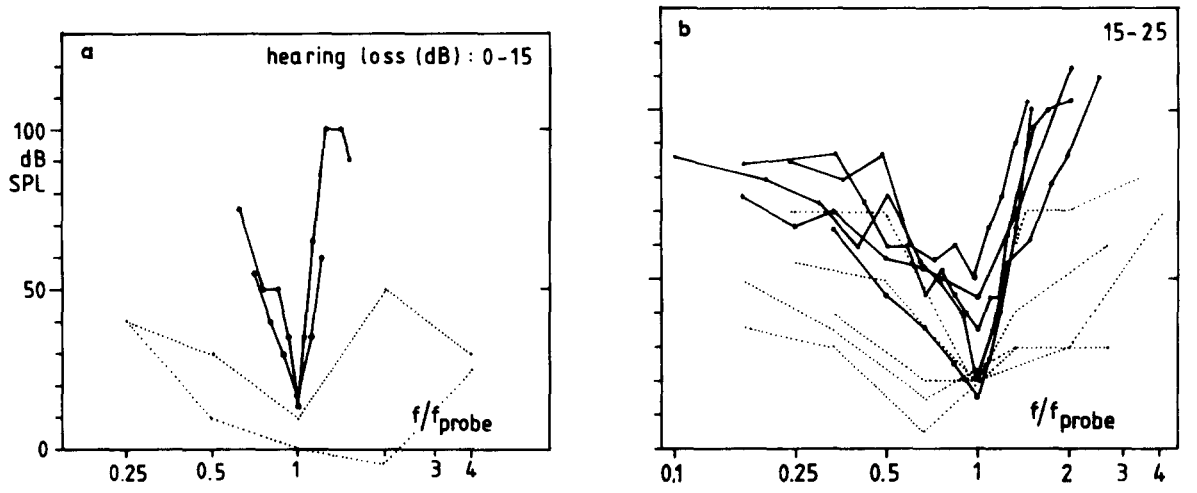

Fig. 2. (a) APTCs in the 0–15 dB hearing loss (at f_{probe}) category. Probe frequency is 2 kHz in both cases. Dotted curve connects AP-thresholds. The frequency axis has been normalized to f_{probe}. (b) Same as (a) for 15–25 dB loss category. Probe frequency is 2 kHz ($N = 2$) or 3 kHz ($N = 3$).

Tuning curves were parameterized by five measures. First, Q_{10dB}, which equals the ratio tip frequency/frequency width at 10 dB above tip level. Secondly, a measure for the slope above the tip frequency determined as a straight line approximation from tip to a 10–20 dB higher level. Third, the same measure but below the tip frequency. We will refer to both measures as the high frequency 'steep' slope and low frequency 'steep' slope, or hf_s and lf_s (dB/octave). Fourth and fifth measures were the 'overall' hf and lf slopes (hf_0 and lf_0), approximated as straight lines from tip level to about maximum of the slope (dB/octave).

In Figs. 5 and 6, Q_{10dB} and hf_s are plotted versus hearing loss, together with their median values. Median values in Fig. 5 drop remarkably steeply for the low-loss groups, above 20 dB the overall trend is still a decrease from $Q = 3.2$ to $Q = 2.7$. Median values of hf_s in Fig. 6 decrease

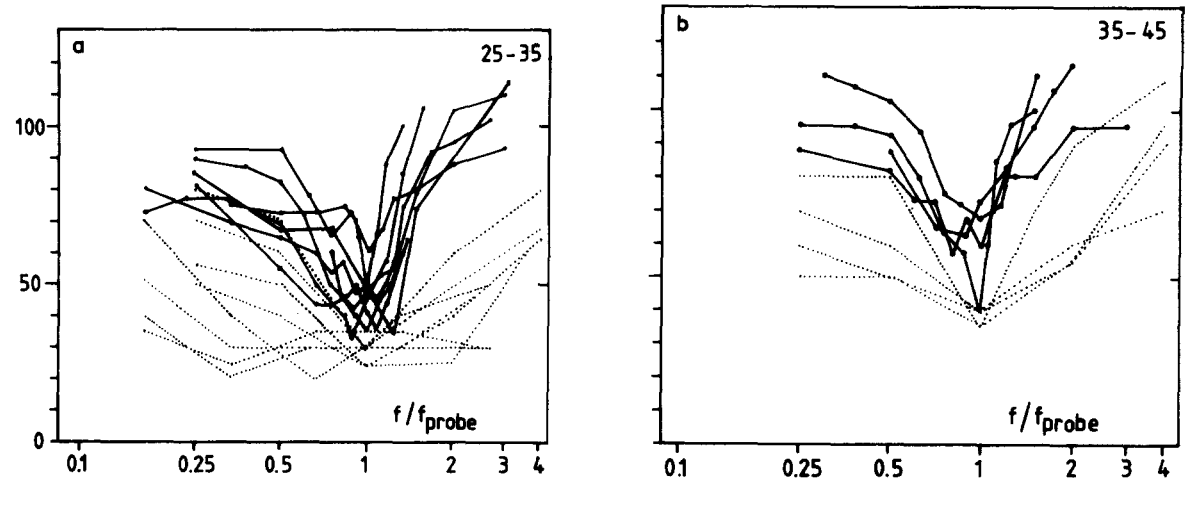

Fig. 3. (a) Same as Fig. 2a for 25–35 dB loss category. Probe frequency is 2 kHz ($N = 4$) or 3 kHz ($N = 4$). (b) Same as Fig. 2a for 35–45 dB loss category. Probe frequency is 2 kHz ($N = 4$).

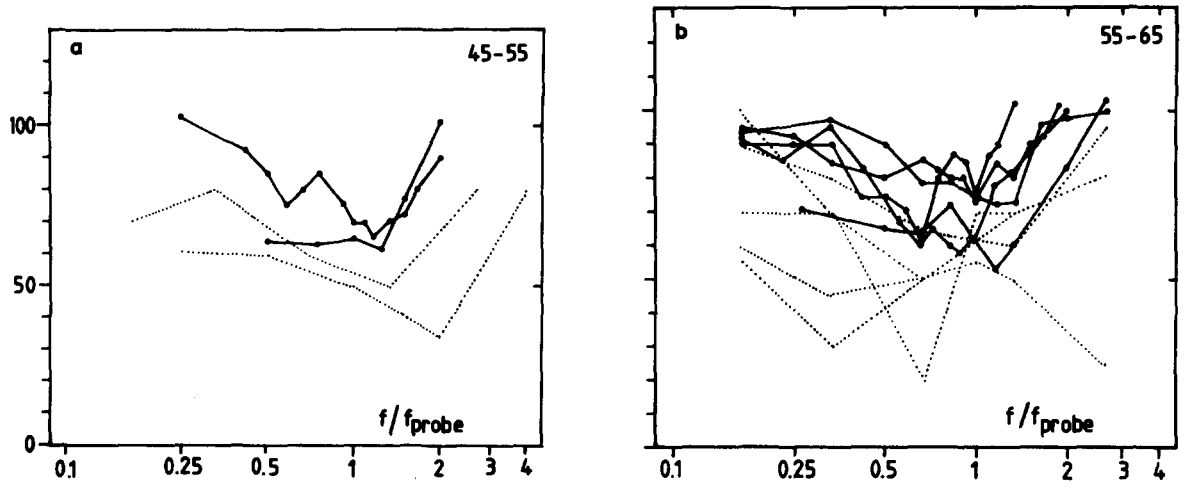

Fig. 4. (a) Same as Fig. 2a for 45–55 dB loss category. Probe frequency is 2 kHz ($N = 1$) or 3 kHz ($N = 1$). (b) Same as Fig. 2a for 55–65 dB loss category. Probe frequency is 3 kHz ($N = 5$).

more gradually up to 50 dB, then a slight increase can be observed.

Fig. 7 shows median values of all five measures; Q_{10dB}, hf_s, lf_s, hf_0 and lf_0. The same decreasing trend can be observed for all five variables. Only for hf_0 is this decrease monotonous, the other curves show a local maximum at 30 or 40 dB hearing loss.

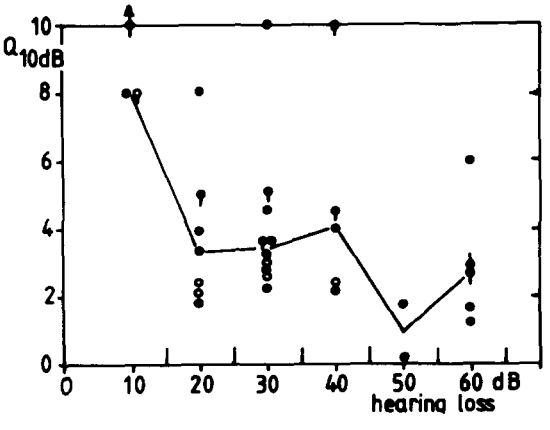

Fig. 5. Quality factor of APTCs versus hearing loss categories. Filled circles are Q_{10dB} values of APTCs in Figs. 2, 3 and 4, i.e., for probe levels within 30 dB from threshold. Open circles ($N = 6$) are for elevated probe levels (see Table I). Small 'tail' segments at circles indicate that the hearing loss strongly increased by more than 20 dB/octave above f_{probe} (7 subjects ♀, ♀) or below f_{probe} (one subject ♀). The curve connects median values in each hearing loss category.

To investigate a possible effect of probe tone level on the tuning curve's quality factor, a second tuning curve at a 30 dB higher probe tone level was measured in five subjects (see Fig. 8). Parameters of both curves in each subject are presented in Table I. On average these data yield a decrease in Q_{10dB} of 1.2 per 30 dB, which is comparable to the decrease in Q_{10dB} from 30 to 60 dB hearing loss in Fig. 7.

A Student t-test was applied to determine if the

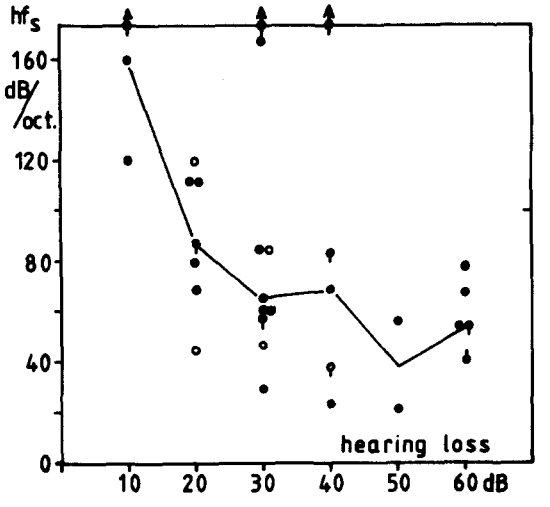

Fig. 6. High-frequency slope near the tip of APTC versus hearing loss categories. Symbols are the same as in Fig. 5. The curve connects median values in each hearing loss category.

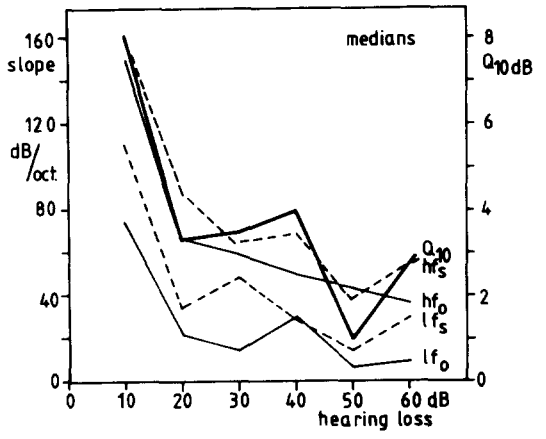

Fig. 7. Medians of slopes (left ordinate) and Q_{10dB} (right ordinate) versus hearing loss categories.

mean Q_{10dB} from Table I at 80/85 dB SPL differed statistically from the mean Q_{10dB} in subjects with 60 dB hearing loss (Fig. 5). Upon leaving out the rather extreme $Q = 6/60$ dB item (see Fig. 5) the t-test shows that the two means are different (statistically significant) at the $\alpha = 0.05$ level, but not at the $\alpha = 0.1$ level. So, this implies that part of the relation between Q_{10dB} and hearing loss is due to probe tone level variation.

In 21 subjects, derived response measurements (or NAPs) were performed. In each subject, NAP latencies, τ, determined at the same frequency, f, as the probe tone frequency in the tuning experiments (i.e., 2 or 3 kHz), were converted to number

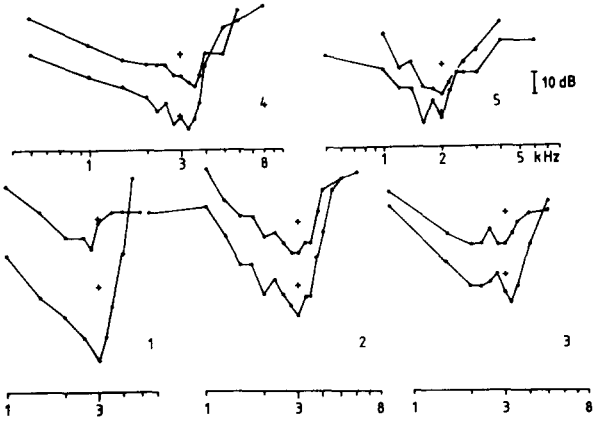

Fig. 8. AP tuning curves in 5 subjects at two probe levels. Subjects are listed in Table I. The probe tone is indicated by +.

TABLE I

Subject	Hearing loss category (dB)	Probe levels (dB SPL)	Q_{10dB}
1	15–25	50/80	4/2.4
2	15–25	50/80	3.3/2.1
3	25–35	55/85	3.2/2.6
4	25–35	50/80	2.8/2.6
5	35–45	60/85	4.5/2.2

of periods N_{NAP} according to the equation $N_{NAP} = (\tau - 0.8)f$, in which 0.8 ms is the assumed synaptic delay (Eggermont, 1979). Fig. 9a presents these N_{NAP} values versus hearing loss. The majority of N_{NAP} values falls within the range for normals, indicated by the bar at the left. This normal range has been taken from a group of 45 normal subjects and equals the range obtained by Eggermont (1979). The drawn curve in Fig. 9a connects median values in each hearing loss category.

Fig. 9b clearly illustrates that a one-to-one relationship between median of Q_{10} and N_{NAP} does not exist. This relationship also does not exist intra-individually, as appears when Q and N_{NAP} are related one by one in each individual.

It is of interest to see in which respect a linear-filter model fails to describe accurately the dependence of N_{NAP} upon filter slopes hf_s and lf_s. To this purpose, in Fig. 10 N_{NAP} has been plotted

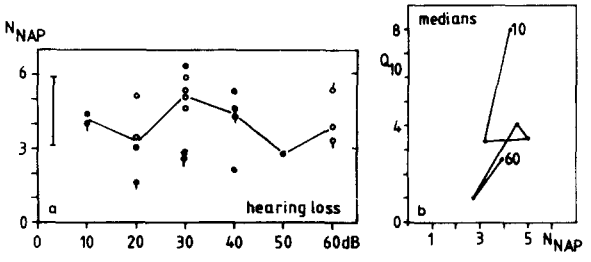

Fig. 9. (a) Number of periods N_{NAP} of derived responses in the 2 (●) and 3 kHz (○) characteristic frequency (CF) region. Drawn curve connects medians. The bar at the left shows normal variation over 2 and 3 kHz region. Tail segments as in Fig. 5. Number of periods has been calculated from NAP latency according to $N_{NAP} = (\tau_{CF} - 0.8)\ f_{CF}$. (b) Medians of Q_{10dB} from Fig. 7 versus N_{NAP} of Fig. 8 with hearing loss as a parameter.

versus the sum of slopes $hf_s + lf_s$. Smooth drawn curves are theoretical prediction of N_{NAP}, according to the equation (see Appendix, eqn. (2)).

$$N_{NAP} = \frac{\beta}{\pi^2}\left(\frac{hf_s + lf_s}{12} - 1\right) \times \left[\ln\left\{\frac{hf_s + lf_s}{12}\right\} + 2\right]$$

in which β is an adjustable parameter. With $\beta = 1$, neural firing is assumed to take place at the maximum of the impulse response, i.e., at neural threshold condition. Fig. 10 shows that at near normal hearing thresholds (10 dB) $\beta = 0.5$ fits best to the experiments, while at 40–60 dB hearing loss $\beta \approx 2$ fits best. The latter result would imply a latency of twice the duration to maximum of the impulse response, which is completely beyond the maximum.

The dashed curve in Fig. 10 connects the same data as used for the drawn one just above it, except that an additional correction to N_{NAP} has been applied, accounting for the (estimated) mechanical traveling wave delay, N_{mech}, i.e.,

$$N_{NAP} = (\tau_{NAP} - 0.8) f_{CF} - N_{mech}$$

with $N_{mech} = 1.7$ periods for 2 kHz and $N_{mech} = 3.3$ periods for 3 kHz. These estimates are the lowest 'worst cases' in Fig. 9a. As a comparison, Eggermont (1979) estimates $N_{mech} = 1.9\ f^{0.3}$ (f in kHz), yielding 2.3 at 2 kHz and 2.7 at 3 kHz. This additional subtraction probably leads to a better estimate of the pure filter delay. The medians for 40–50 dB now are best approximated by $\beta = 1$, indicating that neural firing occurs at the top of the impulse response.

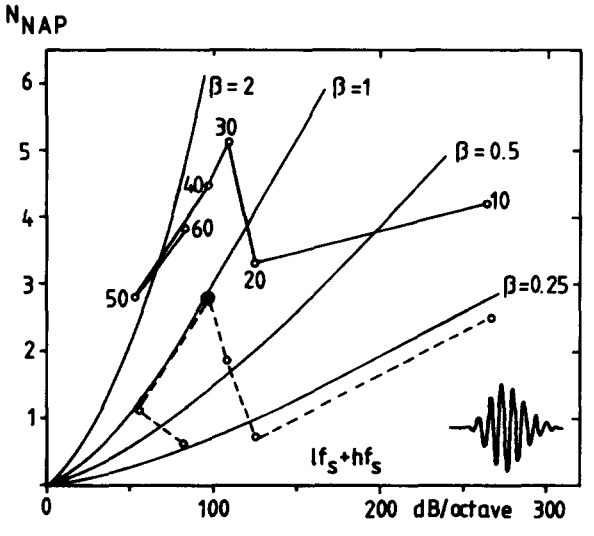

Fig. 10. Open circles, connected by drawn segments are medians of N_{NAP} (Fig. 9a) plotted versus $lf_s + hf_s$ (Fig. 7). The same data, but now additionally N_{mech} subtracted from N_{NAP} (see text), are plotted below and connected by dashed segments. Smooth drawn curves, marked by parameters $\beta = 0.25$ to $\beta = 2$ are theoretical curves predicting number of periods of the impulse response (filter delays) from the sum of slopes (horizontal axis) of the fiber's attenuation curves. For details, see text.

Discussion

Tuning

With regard to Q_{10dB}, the 'normal' value we obtained at 10 dB loss, is higher than Harrison et al. (1981) obtained, 8 versus 2.3, respectively. In the 50–60 dB loss range, Q_{10} values are more comparable, although our values are still higher. Note that we used a 50% reduction criterion, while Harrison et al. used 25%. As reported by Van Heusden en Smoorenburg (1981) a higher masking criterion causes Q_{10} to increase, so this effect might explain part of the discrepancies. On the other hand, our 'normal' results (two subjects, both at 2 kHz, see Fig. 2) were obtained with a detailed frequency spacing around f_{probe}, while Harrison's plots (his Fig. 10) are more 'coarse grained', leading possibly to an underestimation of Q_{10}.

One of our two 'normal' subjects had a strong increase of hearing loss (40 dB/octave) above the probe frequency. This might explain the extreme steep high-frequency slope (280 dB/octave) and high Q_{10} ($= 20$), which explanation is corroborated by the fact that Q_{10} dropped to 8 when the probe level was increased by 30 dB (see Fig. 5, ♀, ♀). As this is a singular, extreme example, we left this sloping audiogram case out of Table I, so in that table only (near) flat audiograms have been included.

In this study, absolute probe level has been shown to be an undoubtly important parameter in the measurement of frequency selectivity. The AP-literature is contradictory at this point, for

example the results in the cat of Gorga and Abbas (1981) versus those of Van Heusden and Smoorenburg (1981). Both used forward masking, although with a different time delay between masker and probe.

The single fibre results in the cat (Møller, 1983) very clearly illustrate that Q_{10} decreases as a function of probe level. For example, Q_{10} at a CF of 1 440 Hz decreases from 1.8 at 10 dB to 1.2 at 30 dB (and then remains constant up to 70 dB) or from about $Q = 4$ at 10 dB to $Q = 1$ at 60 dB (read from Møller (1983), Fig. 2). Q_{10} resulted from Fourier transforms of the cross-correlation function between synthesized ternary sequence noise input and neural histogram output. Thus, in contrast to the conventional single fibre frequency threshold curves, this method also allows measurement of frequency selectivity far above threshold.

Comparing Møller's data with our own (assuming this is valid, considering different neural levels, procedures and species) it appears that his decrease ratio of 4 between 10 and 60 dB (his Fig. 2) is about the same as in our median Q_{10} values (Fig. 5). Our probe level variation experiments yield an average decrease in Q of 1.2 between 50 and 80 dB stimulus level (Table I), while Møller finds a decrease in Q of about 0.8 between 30 and 60 dB.

It seems until now that frequency selectivity is a probe-level dependent property, which is not due to masking procedures as Møller does not use masking. In this respect it is also noteworthy that Lufti (1984) concludes from psychophysical experiments that there are no essential differences between forward and simultaneous masking except for a simple scaling factor. Also, Pickles (1984) concludes that (in guinea pig) non-linearities hardly influence sharpness of tuning below CF and are moreover resistant to cochlear pathology (see also Kuper and Rutten, 1983).

If the frequency transfer curve varies with probe level, in first instance a linear filter approach is not valid as this requires a level-independent, constant filter impulse response. However, as also suggested by Møller (1983), it might be that the linear approach is valid at each level because only the *parameters* of linear tuning are varied by the probe tone level. Then, each level has its own impulse response which does not vary as long as probe level is constant.

Having accepted the observations in Lufti (1984), Møller (1983), Pickles (1984) and in this work, it is evident that nonlinearities play a smaller or different role than hitherto assumed in the change in spectral selectivity. Only the probe level should induce the setting of the parameters of the filter (Møller suggests a relatively slow adaptation time for this setting). This item of parametric control of filter characteristics seems to fit in the experiments on acoustic emissions. It was proposed earlier (Rutten and Buisman, 1983) to model the cochlea 'in terms of non-linear feedback amplifiers of which the feedback factor can be modified externally (by stimulation) or internally (by parameter variation)'. The difference of course is that here we aim at a linear description, while in the emission paper the non-linearity was a central theme. Both approaches together may seem contradictory, however, one should keep in mind that control and existence of emissors already ends at about 25 dB SPL, while the linear approach in this paper runs between 10 and 60 dB SPL.

The foregoing results and discussion make clear that hearing loss is certainly not the only factor which plays a role in determination of cochlear frequency selectivity. Probe level is just as important.

Narrow band action potentials

The relatively great importance of probe level as concluded from the foregoing discussion on tuning, gives rise to expectation that high pass noise masking of a 90 dB pe SPL click in normals and abnormals will reflect more the properties typical for 90 dB than those typical for normal or increased thresholds. In fact, the observed independence of N_{NAP} on hearing loss confirms this expectation. In part, this conclusion was also reached by Eggermont (1979) in that about half of his NAP-latencies in abnormals (his sensory loss no. 2 group) were not different from normal. His other 40 dB-loss group no. 1 was selected on the basis of triphasic waveform of derived N_1 responses. In our group such triphasic responses were present in a small minority of four subjects, which makes Eggermont's and our results almost fully comparable.

This independence of NAP-latencies (within

normal variation) in response to 90 dB pe SPL clicks on hearing loss is a second indication that the stimulus level itself parametrically controls the shape of the impulse response. In other words, the NAP experiments at 90 dB pe SPL click level in each hearing loss category will learn more about filter properties at 90 dB and less about the influence of elevated threshold. This also implies that the only meaningful comparison between N_{NAP} and Q_{10} (or sum of slopes $lf_s + hf_s$) can be made at the same stimulus level. As 90 dB pe SPL click corresponds in our experimental setup to about 60 dB SPL spectral level in a half-octave band around 2 or 3 kHz, one must compare to the tuning experiments at 60 dB SPL probe tone level, i.e., in the 35–45 dB hearing loss category. Therefore, in Fig. 10 the 40 dB category data point has been accentuated by a heavy filled circle. One observes that the theoretical fit is best for $\beta = 1$, i.e., on top of the impulse response. Note that the farther away from 40 dB hearing loss, comparison between N_{NAP} and $(lf_s + hf_s)$ values is no longer valid, as both parameters are not determined at the same stimulus level. So, the good fit in Fig. 10 between experimental data at 10/20 dB hearing loss (dashed curve) and the drawn curve for $\beta = 0.25$, is artificial.

Appendix

As an approximation for the impulse response of the hypothetical cochlear filter, Duifhuis (1973) uses (see also Goldstein et al. (1971) and Eggermont (1979))

$$h_{CF}(t) = \frac{(\alpha f_{CF} t)^{n+1}}{tn!} e^{-\alpha f_{CF} t} \cos 2\pi f_{CF} t \quad t \geq 0$$
$$= 0 \quad t < 0 \qquad (1)$$

in which f_{CF} is the characteristic frequency of a fiber, $\alpha = \pi^2/(2 + \ln(n+1))$ and $n = ((hf + lf)/12) - 1$. Slopes hf and lf are the slopes of the corresponding band pass filter in dB/octave. (As an example for $hf + lf = 150$ dB/octave the shape of $h_{CF}(t)/f_{CF}$ is given by the lower-right inset in Fig. 10.) The time to maximum of the envelope of eqn. (1) is easily calculated (neglecting the fine structure of $\cos 2\pi f_{CF} t$, i.e. for slow decay with respect to f_{CF}) as $t_{max} = n/\alpha f_{CF}$ or, in number of periods, $N_{max} = n/\alpha$

$$N_{max} = \frac{1}{\pi^2}\left\{\frac{hf + lf}{12} - 1\right\} \times \left\{\ln\left(\frac{hf + lf}{12}\right) + 2\right\} \qquad (2)$$

By using the ratio $\gamma = hf/lf$ this can be rewritten as:

$$N_{max} = \frac{1}{\pi^2}\left\{\left(\frac{1+\gamma}{12\gamma}\right) hf - 1\right\} \times \left[\ln\left\{\left(\frac{1+\gamma}{12\gamma}\right) hf\right\} + 2\right] \qquad (3)$$

or

$$N_{max} = \frac{1}{\pi^2}\left\{\left(\frac{1+\gamma}{12}\right) lf - 1\right\} \times \left[\ln\left\{\left(\frac{1+\gamma}{12}\right) lf\right\} + 2\right] \qquad (4)$$

As, by definition,

$$Q_{10dB} = \frac{f_{CF}}{f_H - f_L} = \frac{f_{CF}}{f_{CF}\{2^{10/hf} - 2^{-10/lf}\}} \qquad (5)$$

and $2^{10/x} = e^{(10/x)\ln 2} \approx 1 + \frac{6.9}{x} \quad (x \gg 6.9)$

one finds $Q_{10dB} = \frac{1}{6.9}\left(\frac{hf - lf}{hf + lf}\right)$ (6)

Substituting eqn. (6) in eqn. (2) results in

$$N_{max} = \frac{1}{\pi^2}\left\{\frac{6.9}{12}\left(\frac{\gamma+1}{\gamma}\right)^2 Q_{10dB} - 1\right\} \times \left[\ln\left\{\frac{6.9}{12}\left(\frac{\gamma+1}{\gamma}\right)^2 Q_{10dB}\right\} + 2\right] \qquad (7)$$

Acknowledgements

This work was supported by the Heinsius Houbolt fund and the Dutch Organization for the Advancement of Pure Research (ZWO). Stimulating discussion with P. Kuper and technical assistance by A. Van Wijngaarden and P. Schotel are

gratefully acknowledged. Also, we thank the ENT Dept. medical staff for support and T. Steijlen for typing.

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