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Auditory enhancement at the absolute threshold of hearing and its relationship to the Zwicker tone

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Abstract

Auditory enhancement describes an improvement in the detection of a tonal signal in a broad-band masker with a spectral gap at the signal frequency if the signal is delayed in its onset relative to the masker. This auditory enhancement may be based on an increase of the effective signal level instead of a decline in the effective masker level. In order to evaluate whether this signal enhancement also exists at the threshold of hearing, we measured the absolute threshold for pure-tone pulses of different frequencies with and without preceding band-rejected noise. Such noise also causes the sensation of the Zwicker tone – a faint pure tone lasting for a few seconds immediately after the noise presentation. The pitch of this sensation is a complex function of the noise parameters but always lies at a frequency within the rejected band. During the Zwicker tone sensation, auditory sensitivity for tone pulses at frequencies adjacent to the Zwicker tone was improved by up to 13 dB instead of being reduced which might be expected due to the presence of the simultaneously audible Zwicker tone. The failure to influence this threshold shift with low-frequency tones and measurements of the ear's acoustical response indicate that this threshold improvement may be produced through neuronal disinhibition rather than through a release from mechanical suppression in the cochlea.

Keywords: Threshold improvement; Auditory enhancement; Zwicker tone; Negative afterimages; Temporary threshold shift

1. Introduction

Afterimages are primarily known from the visual system. Colored negative afterimages are sensory illusions that often occur following prolonged exposure to constant stimuli. In the auditory system, a negative afterimage is perceived immediately after the presentation of broadband noise at low or intermediate levels with a spectral gap containing no acoustical energy. This afterimage consists of a faint pure-tone sensation lasting for several seconds (Zwicker, 1964; Lummis and Guttman, 1972; Fastl, 1989). The pitch of this 'Zwicker tone' (Lummis and Guttman, 1972) is within the range of the spectral gap and can be accurately predicted by masking patterns (Krump, 1993). The pitch of the Zwicker tone is always at the intersection between the falling slope of the low-pass components of the masking pattern and the threshold in quiet, or at the intersection between the falling slope of the low-pass and the rising slope of the high-pass components of the masking pattern. Therefore the Zwicker tone, emerging at a place in the masking pattern where there was no excitation before, can be regarded as a negative acoustic afterimage of the band-rejected noise. It is not known at which level of the auditory system this afterimage is generated. Since it cannot be produced when the low-pass component and the high-pass component of the band-rejected noise are presented to different ears (Krump, 1993), it is a strictly monaural effect. Thus this negative auditory afterimage may be generated peripherally at the level of the cochlea, or centrally in the monaural stations of the ascending auditory pathways.

Although the Zwicker tone is perceived as a faint sinusoidal stimulus decaying over a few seconds, its perception differs from that of a physically present pure-tone in several ways (Krump, 1993):

1. It was impossible to produce beats or beat-like

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sensations between the Zwicker tone and a sinusoidal stimulus of similar frequency.

2. Although it was possible to mask the Zwicker tone with another tone, it was impossible to mask the perception of a tonal stimulus with a Zwicker tone.
3. It was not possible to measure spontaneous otoacoustic emissions correlated with the Zwicker tone. This means that there is probably no fast mechanical activity in the inner ear that corresponds to the frequency of the Zwicker tone.

The same stimuli that give rise to the sensation of the Zwicker tone are used in auditory enhancement experiments: the simultaneously masked threshold of a pure-tone signal is substantially lower when the masker and the signal are preceded by an adapting stimulus with a spectral gap centered around the signal frequency. The threshold difference is called signal enhancement (see for example Viemeister, 1980; Carlyon, 1987; Wright, 1995). Several suggestions have been made concerning the underlying mechanisms of this psychoacoustical phenomenon (for a review, see Wright, 1995) but the discussion is still open. Viemeister and Bacon (1982) questioned whether the improved detectability of the signal was caused by an increase of the effective signal level or by a decline in the effective masker. They presented a harmonic complex with one harmonic missing. Presenting the complete harmonic complex directly after the incomplete complex leads to an auditory enhancement of the one harmonic that was missing in the first stimulus. Viemeister and Bacon (1982) measured the forward-masking capability of the harmonic depending on whether it was enhanced or not. As the enhanced harmonic showed a considerably stronger forward-masking capability, Viemeister and Bacon concluded that auditory signal enhancement is due to an increase in the effective signal level rather than a decrease in the effective masker level.

The questions we examined in the present study were: is this signal enhancement also measurable without a simultaneous masker? Is the signal enhancement related to the generation of the Zwicker tone that emerges after the same kind of adapting stimulus?

We presented band-rejected noise to human subjects and determined the absolute threshold of hearing during the sensation of a negative afterimage. To gain first insight into the physiological mechanisms that may be related to the psychophysical threshold improvement we found in our first experiments, we measured the influence of band-rejected noise on spontaneous otoacoustic emissions (SOAEs) and we tried to influence the threshold improvement with loud low-frequency tones.

As stated above, the Zwicker tone is an internally generated sensation that is only perceived as a faint pure-tone presented to the ear. The absolute threshold in quiet is a measure of the sensitivity to physical input. Thus, threshold measurements during the sensation of the Zwicker tone were performed in *physical* quiet although the subjects had to detect the pulsed signal superimposed on their Zwicker tone sensation. One has to keep in mind that this superposition does not lead to the perception of beat-like interactions. Furthermore, the pulsed signal and the Zwicker tone were clearly distinguishable due to their different time courses (a relatively fast pulsing signal (see below) and a Zwicker tone slowly decaying within 1.5–6 s).

2. Methods

2.1. Stimuli

For the measurement of the hearing threshold, pure-tone pulses of 130 ms were presented at a repetition period of 260 ms (11 ms raised cosine up and down slopes). On different experimental sessions, the signal was set to a pure-tone frequency between 2.8 and 5.3 kHz. The band-rejected noise (overall bandwidth of 50–18 000 Hz) used to influence the threshold in quiet was generated by digital addition of sinusoids with 3.125 Hz frequency distance and random phase (Krump, 1990). Two spectral gap widths (1400 Hz in experiments I–III and 2900 Hz in experiment IV centered around 4 kHz on a critical band scale) and two overall noise levels (30 and 40 dB SPL) were used. Due to the flat frequency response of the DT48 headphones together with the free-field equalizer (see below), this translates to a frequency-independent spectrum level of −2.2 dB/Hz in experiments I and II, of −12.2 dB/Hz in experiment III and of −1.8 dB/Hz in experiment IV with the increased rejected-band width. As a control, we used broadband noise with the same sound-pressure level.

2.1.1. Signal generation

All signals were digitally generated off-line and played back at a sampling rate of 50 kHz by a dsp32c System board (Loughborough Sound Images, playback routine by V. Nitsche). The sound-pressure levels of the signal and the band-rejected noise were controlled by custom-made programmable attenuators. The sound presentation was monaural using Beyerdynamics Dt48 headphones and a passive free-field equalizer (Zwicker and Fastl, 1990) which equalizes the DT48 headphones to have a flat frequency response relative to a free-field sound presentation. All stimuli were checked using a B&K 2610 Measuring Amplifier and a HP 3561A Dynamic Signal Analyzer.

2.2. Subjects and procedure

Five subjects aged 24–30 years (all with normal hear-

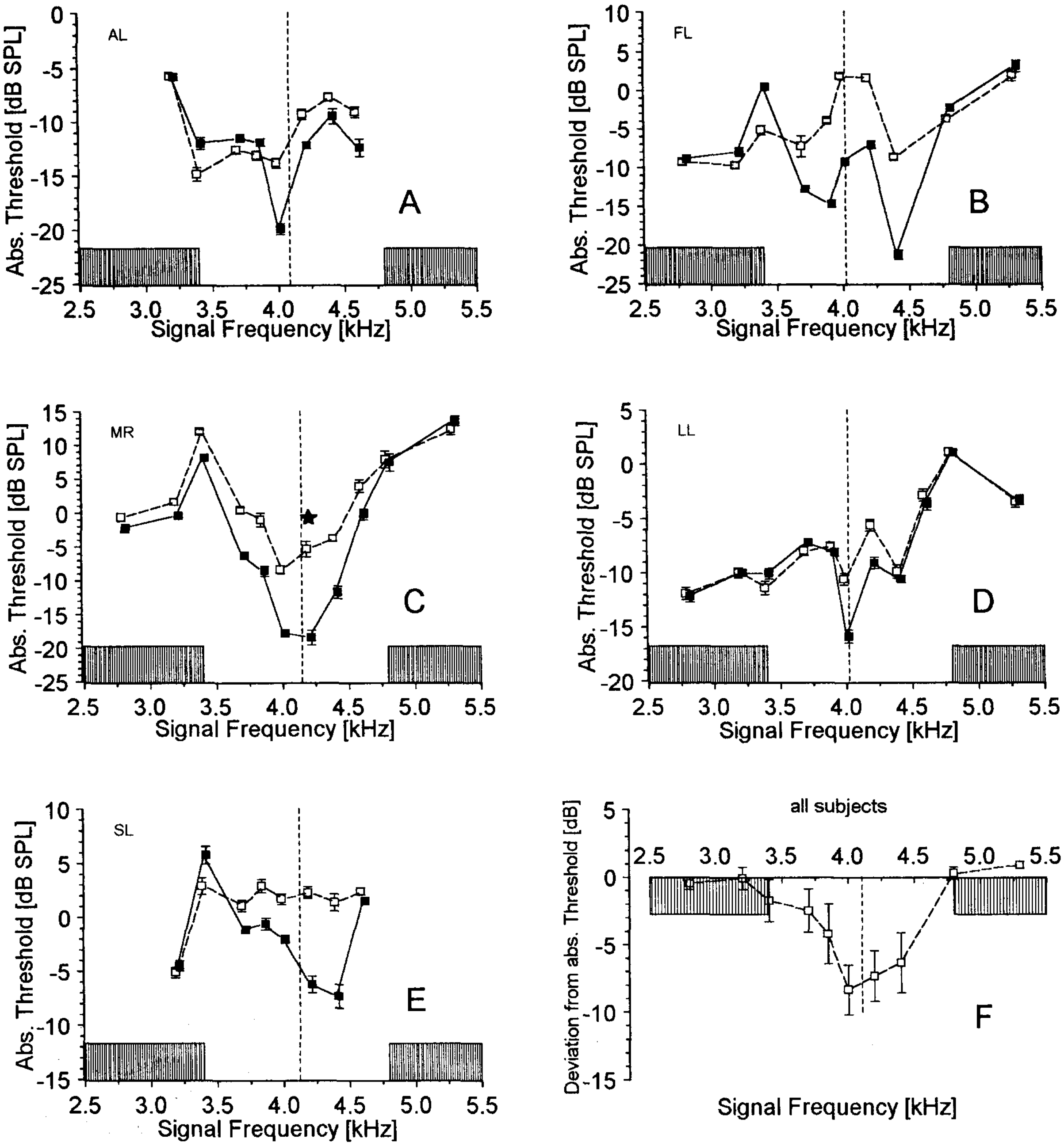

Fig. 1. A–E: absolute threshold of hearing for 130 ms tone pulses presented at a 260 ms repetition rate in physical quiet for 5 subjects. The open symbols and dashed line show the uninfluenced thresholds as a function of signal frequency. The filled symbols and the solid line represent the absolute thresholds during the sensation of the negative afterimage elicited by the band-rejected noise. The error bars show the standard error. The pitch of the Zwicker tone is given by the vertical dashed line. The spectral edges (3.4 and 4.8 kHz) of the band-rejected noise (50–18 000 Hz) are indicated by the two vertically hatched boxes. The star in C indicates the threshold estimate of a control measurement with broadband noise instead of band-rejected noise. F shows the deviation of the absolute threshold in quiet after the presentation of band-rejected noise averaged over 5 subjects (all with normal hearing) within the spectral gap and over 3 of the 5 subjects at the edges and outside the spectral gap. The curve is normalized setting the uninfluenced threshold to 0 dB. The band-rejected noise is indicated by the two vertically hatched boxes. The Zwicker tone averaged for all subjects is given by the vertical dashed line. The maximum threshold improvement at 4.0 kHz is −8.4 dB ± 4.1 dB. At frequencies between 4.0 kHz and 4.4 kHz, the thresholds obtained after the band-rejected noise presentations were significantly lower than those determined without band-rejected noise (*t*-test for dependent samples, $P < 0.05$; df = 3).

ing) took part in experiment I, three of them in experiments III and IV. One experimental session consisted of 3 measurements. All of them were performed with a modified von Békésy tracking paradigm, i.e., the subjects had to lower the signal level if they heard the signal and to raise the level if they did not. For each of the 3 measurements, the tracking procedure was continued until 11 reversals (a transition from decreasing to

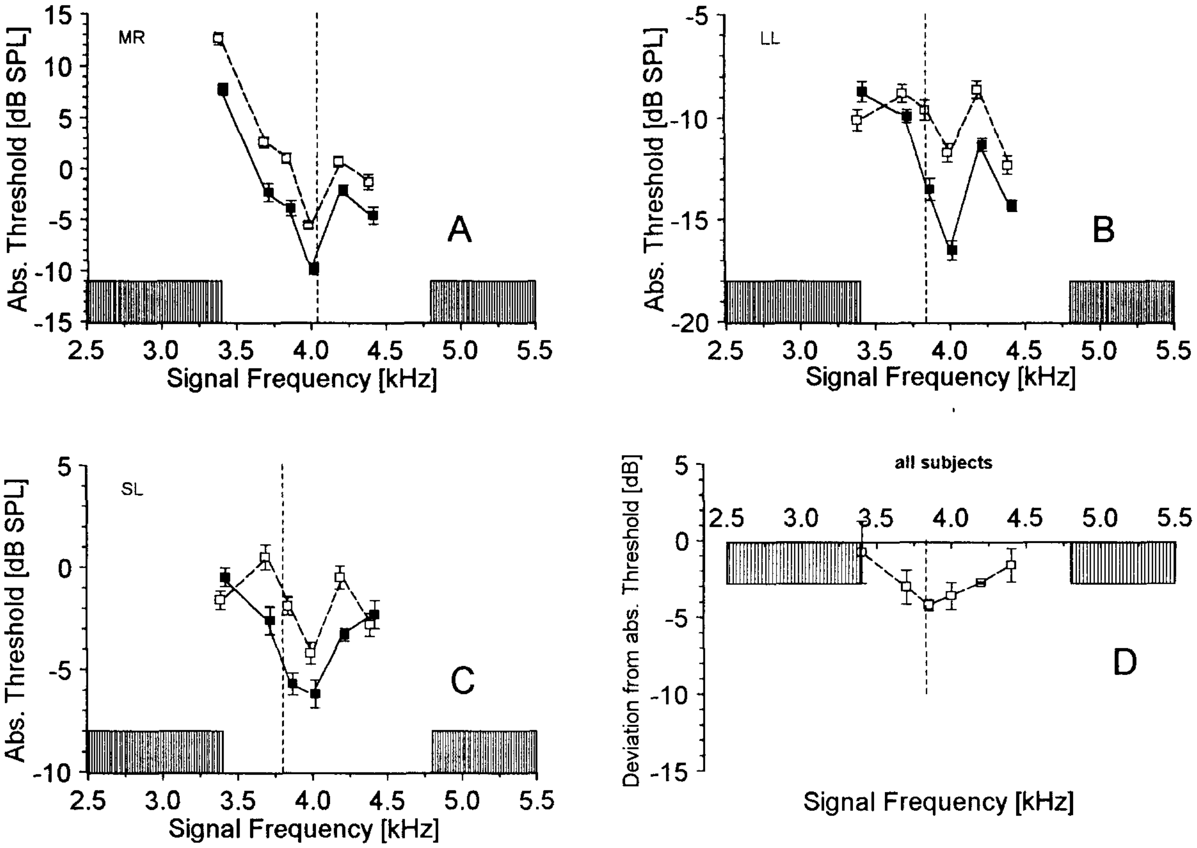

Fig. 2. A–C: experiment III. Results from 3 subjects for a band-rejected noise level of 30 dB SPL. D shows the averaged deviation from the uninfluenced threshold in quiet averaged for all 3 subjects tested (for further explanation see Fig. 1).

increasing level or vice versa) were obtained. The first 5 reversals were discarded, the final 6 reversals were stored.

In the first and the third measurements within one session, the pulsed signal was presented continuously at a repetition frequency of 3.8 Hz, starting with a sensation level that was randomized between 20 and 40 dB SL. The subjects determined the uninfluenced threshold in quiet for the pulsed signal with the tracking procedure using a step size of 2 dB.

In the second measurement within each session, the influence of the band-rejected noise was studied using a modified procedure. The tracking procedure was split into a sequence of trials. A trial consisted of a noise presentation immediately (0 ms delay) followed by a 2 s presentation of the pulsed signal at a given level. The repetition frequency of the pulse train was the same as in measurements 1 and 3. In the first trial of measurement 2, the signal level was set to a random level of 4–10 dB above the threshold determined in measurement 1. In the following trials, the signal level was decreased in steps of 1 dB until the subject reported not to hear the signal. Then, the signal level was increased by 1 dB in the next trial. The subjects could reduce the signal level by 10 dB in a single step to assure the perception with no audible signal present. As in measurements 1 and 3, 11 reversals of the signal level changes were obtained and thresholds were calculated in the same way. The thresholds shown for each signal frequency in each experiment were obtained from at least 3 sessions on different days. The duration of the noise presentation was selected individually by the subjects to elicit a good Zwicker tone sensation but typically ranged from 2 to 3 s.

The pitch and loudness of the Zwicker tone were estimated by adjusting the frequency and level of a comparison tone applied to the contralateral ear.

In experiment II, the results of experiment I were checked using a 2-alternative forced-choice (2-AFC) procedure. Each observation interval was preceded by a 1 s broadband noise or band-rejected noise presentation with the same spectral composition and level as in experiment I. The signal was a train of four 125 ms pure-tone pulses with 125 ms pauses presented after the band-rejected noise with zero delay between the noise envelope and the envelope of the first signal pulse. The last pulse of the train started with a 750 ms delay from the end of the noise which is considerably longer than the time range of forward masking. In successive trials, the signal level was changed according to a 3-down 1-up rule estimating 79% correct responses. The step size was 5 dB for the first two reversals and it was stepwise reduced to 1 dB after the fifth reversal. Thresholds were determined using the last 6 reversals of the threshold changes (step size of 1 dB). At least 3 runs per signal frequency were performed with spectrally flat noise and with band-rejected noise preceding the signal, respectively. Four subjects – three of them different from those of experiment I – took part in this control experiment. The subjects (2 females and 2 males) were between 24 and 30 years old and had absolute thresholds between −3 and 12 dB SPL at 4 kHz.

3. Results

In the first experiment, broadband noise with a spectral gap between 3400 and 4800 Hz was presented at an overall level of 40 dB SPL. Noise stimuli of comparable level and spectral gap width were used by Krump (1993) to elicit a maximum sensation level of the Zwicker tone.

The results from 5 subjects are shown in Fig. 1A–E. The subjects showed a significant temporary threshold improvement for signal frequencies within the spectral gap directly after the presentation of band-rejected noise. The maximum improvement varied between 5.3 and 13.1 dB among the subjects. Fig. 1F shows the averaged threshold improvement for all subjects. It amounted to 8.4 dB at 4 kHz, close to the average pitch of the Zwicker tone which was 4.14 kHz. It is important to note that we never observed an improvement if we used signal frequencies outside the spectral gap of the preceding noise or if we used spectrally flat noise instead of band-rejected noise (cf. start in Fig. 1C). The subjects were not informed about these parameters. For these experimental conditions, we found the expected forward masking that suppressed the perception of at least the first signal pulse after the noise presentation. Nevertheless, the subjects did not always show an elevated threshold due to this forward masking because the pulsed signal presentation lasted 2 s and the subjects obviously focused their attention on the part of the observation interval following the forward-masking effects. In the conditions in which we found a threshold improvement, the subjects described their sensation as the signal 'riding' on the Zwicker tone. The Zwicker tone and the signal were clearly distinguishable due to their different temporal structures: the Zwicker tone decayed slowly and remained continuously audible for about 1–3 s whereas the signal was pulsed at a repetition rate of 260 ms.

The 2-AFC control experiment was designed to ensure that the threshold improvements found in experiment I were not caused by shifts in the decision criterion of the subjects. As shown in Table 1, an improvement in the pure-tone absolute thresholds during the Zwicker tone sensation was found for all of the 4 subjects tested. The 1 subject that took part in both experiments showed an improvement of 5.3 dB in experiment I. In the 2-AFC control experiment, the maximum threshold improvement amounted to 4.0 dB at the same signal frequency. The other 3 subjects tested with the 2-AFC paradigm showed a threshold improvement of 9.5 dB, 7.9 dB, and 6.3 dB, respectively. The average maximum threshold improvement measured with the 2-AFC paradigm amounted to 6.9 dB at a signal frequency of 4 kHz. As in experiment I, no improvement was found for signal frequencies outside the spectral gap in any subject (cf. threshold differences for a signal frequency of 3 kHz in Table 1).

Three of the 5 subjects of experiment I took part in experiments III and IV. In experiment III, the stimulation was the same as in experiment I except using a band-rejected noise level of 30 dB SPL, i.e., 10 dB lower than in experiment I. The average pitch of the Zwicker tone shifted to about 3.8 kHz (cf. Fig. 2A–C). This shift to a lower frequency is predicted by the model for the pitch of the Zwicker tone because the masking pattern of the low-pass components of the band-rejected noise spreads less into the spectral gap. The threshold shift was still present but smaller (cf. Fig. 2D). Along with

Table 1

Results of experiment II: influence of a preceding presentation of band-rejected noise on the pure-tone absolute threshold of a train of four 125 ms pure tone pulses measured with an adaptive 2-AFC paradigm

Subject	Signal frequency	Threshold and standard errors after white-noise presentation (dB SPL)	Threshold and standard errors after band-rejected noise presentation (dB SPL)	Threshold improvement (dB)
LR	3.0	−6.1 ± 0.6	−6.7 ± 0.2	0.6
BR	3.0	7.0 ± 0.3	8.7 ± 0.3	−1.7
AR	3.0	−4.8 ± 0.7	−1.3 ± 0.9	−3.5
LR	4.0	−2.4 ± 0.3	−6.4 ± 0.6	4.0
MR	4.0	6.7 ± 0.5	−1.2 ± 1.1	7.9
BR	4.0	3.1 ± 0.7	−7.4 ± 1.0	9.5
AR	4.0	11.8 ± 0.6	5.5 ± 0.3	6.3

Noise parameters: broadband noise of 50–18000 Hz with or without a spectral gap between 3400 and 4800 Hz and a spectrum level of −2.2 dB/Hz presented for 1 s in each trial. At a signal frequency of 4 kHz, a threshold improvement was found for all 4 subjects tested whereas at a signal frequency of 3 kHz, i.e., in a frequency range outside the rejected band, no threshold improvement could be measured.

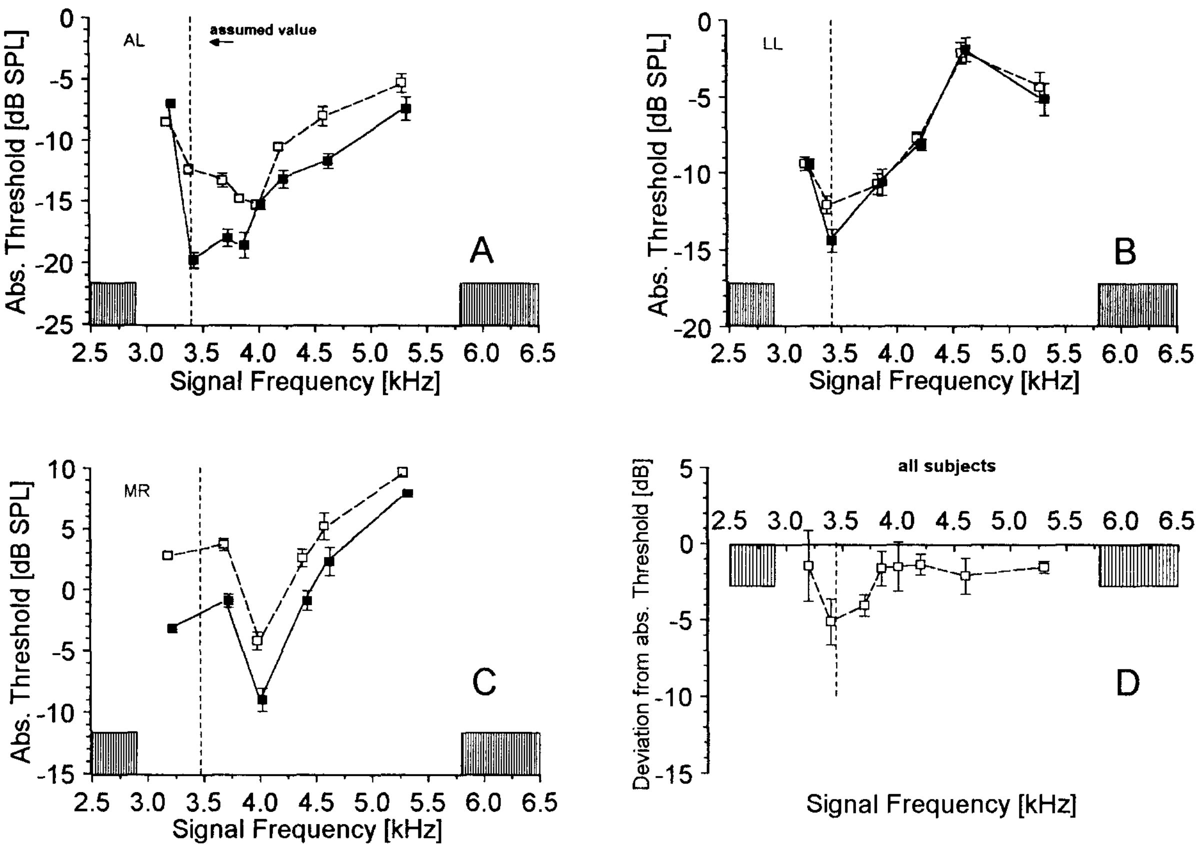

Fig. 3. A–C: experiment IV. The threshold shift of 3 subjects induced by a band-rejected noise with a noise level of 40 dB SPL and an increased spectral gap width of 2900 Hz (2.9–5.8 kHz). D again shows the averaged deviations from the uninfluenced threshold in quiet.

the change of the pitch of the Zwicker tone, the frequency of the highest average threshold improvement of 4.3 dB decreased to 3.85 kHz.

Increasing the bandwidth of the spectral gap to 2900 Hz (2.9–5.8 kHz; noise level: 40 dB SPL) in experiment IV led to similar changes (Fig. 3A–D). Again in agreement with the above mentioned model, the average frequency of the Zwicker tone fell to 3.45 kHz. The averaged maximum threshold shift amounted to −5.2 dB at 3.4 kHz.

4. Additional observations

The following experiments were designed to give a first insight into possible influences of cochlear mechanics on the generation of the Zwicker tone and the signal enhancement at the absolute threshold. First, we investigated the influence of band-rejected noise on spontaneous otoacoustic emissions (SOAEs) and secondly, we wanted to find out if low-frequency biasing stimuli interfere with the perception of the Zwicker tone and the signal enhancement at the absolute threshold.

The measurements of spontaneous otoacoustic emissions were recorded with a Etymotic Research ER10B apparatus and a HP3561A Dynamic Signal Analyzer. For the low-frequency masking experiments, modified AKG K270 headphones were used: these headphones with circumaural cushions and a closed volume behind the drivers were connected to a 12-inch woofer via a 0.5-inch tubing. Spectrum and sound-pressure levels of the low-frequency masker were checked with a flat-plate coupler and a Brüel & Kjaer 4165 microphone.

One subject had two SOAEs, one of them at 1.642 kHz with a level of 6 dB SPL (see Fig. 4A). The sound-pressure level of this SOAE was measured in the closed ear canal before, during, and after the presentation of band-rejected noise with a gap width of 2 critical bands (1480–2000 Hz). Directly after the presentation of a band-rejected noise, the subject described a substantially stronger loudness sensation of the SOAE. Based on the subject's statement, the perceived loudness of the SOAE decreased to its uninfluenced value with a similar temporal decay as the Zwicker tone. In agreement with previous investigations on SOAEs (e.g. Zurek, 1981), the sound-pressure measurements in the closed ear canal showed that the SOAE was strongly suppressed during the noise presentation, probably because of suppressive interaction in the cochlea (see Fig. 4B). Fig. 4C shows the level of the SOAEs measured in a 400 ms interval directly after the end of the noise presentation, i.e., in a time interval, in which the sensation caused by

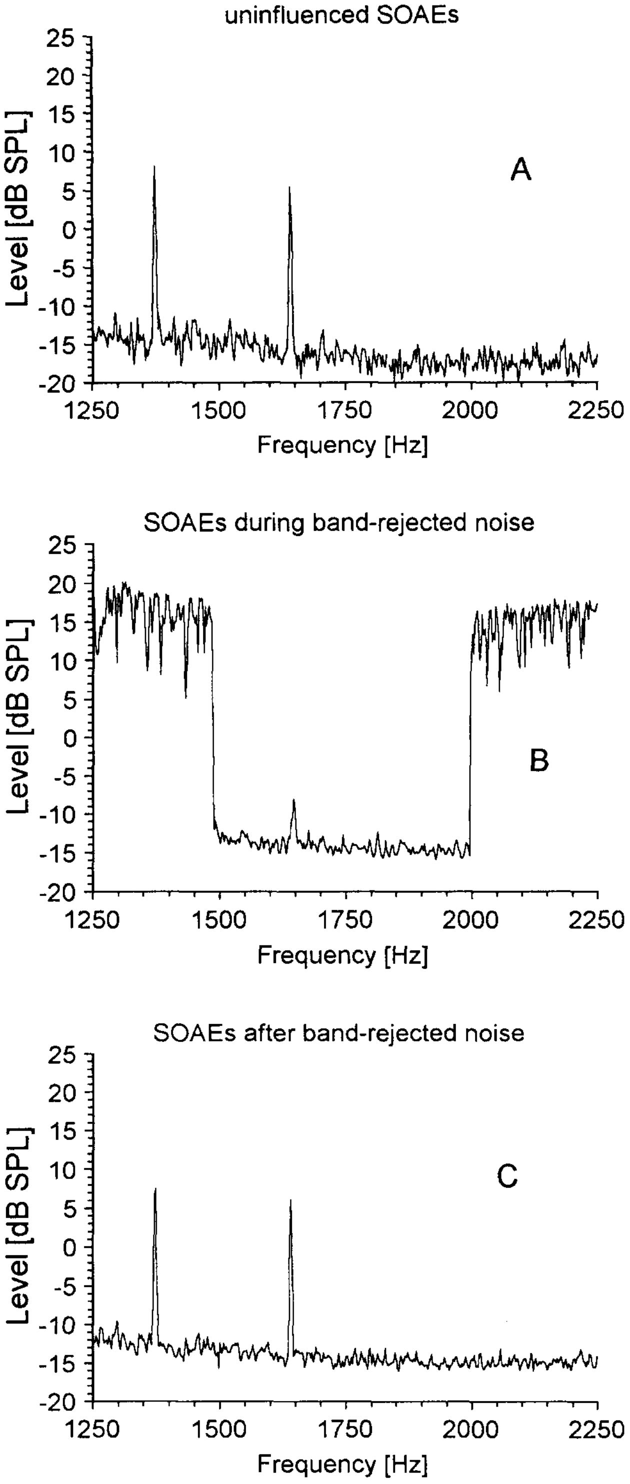

Fig. 4. Spontaneous otoacoustic emissions (SOAEs) of 1 subject: all measurements are averaged over 20 records. A shows 2 SOAEs, one of them of 6 dB SPL at 1642 Hz. B shows data from the same subject during the presentation of a band-rejected noise (spectral gap between 1480 and 2000 Hz). The SOAE at 1642 Hz is strongly suppressed by the noise. C shows the SOAEs recorded at a time interval of 400 ms beginning directly after the end of the noise presentation. Although the perception of the SOAE at 1642 Hz was strongly enhanced, the sound-pressure level of the SOAE was not increased.

the SOAE was significantly increased. Nevertheless, the measured sound-pressure level of the 1642 Hz emission remained unchanged from before the noise presentation. From several studies on the temporal recovery of SOAEs after suppression caused by high level pure tones at frequencies below the SOAE frequency, it is known that full recovery may last up to 10 min (e.g. Norton et al., 1989). The fast recovery seen in our observation is probably due to the relatively faint band-rejected noise. The increased loudness perception of the SOAE, however, perceived after the presentation of band-rejected noise with the spectral gap centered around the SOAE frequency and reported first by Krump (1993) is not caused by an increase in the measured SOAE level. This means that, whereas the physical source of the sensation is not increased in level, the sensitivity with which the source is perceived is increased after band-rejected noise. Based on this observation, it may be hypothesized that the physiological correlate to the increased perceptual sensitivity is different from cochlear amplification which is probably responsible for the generation of SOAEs.

To evaluate hypotheses that put auditory enhancement and the Zwicker tone in the context of relatively slow mechanical interaction in the inner ear, we additionally measured thresholds after presentation of band-rejected noise and simultaneously presented low-frequency pure-tone biasing stimuli of 5–50 Hz with 80–120 dB SPL. Similar stimuli were used for example by Zwicker (1983) to change the level of evoked otoacoustic emissions and to induce positive and negative threshold shifts (Zwicker, 1977). The results of this experiment are shown in Table 2. Neither the perception of the Zwicker tone nor the threshold shift were significantly influenced by the low-frequency stimuli. This is a second hint that cochlear mechanics do not interfere directly with the generation of the Zwicker tone or the accompanying increased sensitivity.

5. Discussion

The experiments presented show that during the sensation of the Zwicker tone the absolute threshold of hearing can be significantly improved by up to 13 dB. The improvement is most pronounced at frequencies in the vicinity of the frequency of the Zwicker tone sensation and it is absent for frequencies outside the spectral gap. The threshold improvements were found both with a modified tracking procedure and using an adaptive 2-AFC method; thus they cannot be accounted for by a shift in the decision criterion or other procedural effects.

Miskiewicz et al. (1994) demonstrated that procedural effects can be responsible for a lowering of the absolute threshold following an adapting stimulus. They replicated experiments originally performed by Zwislocki et al. (1959) and Rubin (1960) using 80 ms 20 dB SL cue tones and variably delayed 20 ms test tones of the same frequency. Whereas a threshold improvement for the test signal was observed with a tracking paradigm, no improvement was found using a 2-AFC paradigm. As the threshold improvement we found in the current experiments was in the same order of magnitude for both experimental paradigms, our results are obviously not influenced by procedural effects. The results of Miskiewicz et al. (1994) render it also unlikely that the threshold improvement may be caused by the Zwicker tone just cueing the subjects to the signal frequency. If cueing was responsible for the threshold improvement, an improvement would also have to be seen using the 2-AFC paradigm in Miskiewicz et al.'s experiment.

A sensitization of the auditory system at the absolute threshold has been reported in several studies concerning the effects of long-term exposure to stimuli of low or intermediate level (e.g. Moore, 1968; Melnick, 1969; Noffsinger and Olsen, 1970; Noffsinger and Tillman, 1970). In these studies, auditory sensitivity is enhanced by up to about 4 dB 40–60 s after the end of an exposure tone that had lasted between one and several minutes. Due to the large differences in the time course of stimulation, however, these effects are not directly comparable to our results.

Viemeister and Bacon (1982) also looked for changes in the absolute threshold of a 30 ms pure-tone signal after the presentation of stimuli with a spectral gap centered around the frequency of the signal. Instead of the threshold improvement observed in our results, they found a 6–7 dB increase in threshold. This difference may be attributable to the differences in the stimuli used. Their stimulus preceding the signal was a harmonic complex with a fundamental of 200 Hz. The complex was divided into a 500 ms adaptor and a 100 ms masker. The harmonics at 1.8, 2.0 and 2.2 kHz were omitted, i.e., the stimulus contained a spectral gap from 1.6 to 2.4 kHz. The level of each harmonic was set to 43 dB SPL. This means that the stimulus excited the critical bands adjacent to the spectral gap much stronger (about 46 dB per critical band) than our band-rejected noise (about 23 dB per critical band). It is well known (Krump, 1993) that the sensation of the Zwicker tone becomes very weak or is even absent following stimuli of this high critical band levels. Furthermore, the signal was very short and it was presented just once. Thus, the results are strongly influenced by forward masking which was actually the intention of the authors. The time ranges of threshold improvement we found and that of auditory enhancement (Viemeister, 1980) outlast the range of forward masking substantially. Thus it is most promising to look for a threshold improvement at longer delays of the signal and to use a train of pulses instead of just one pulse. These procedural differences to our own study may account for the fact that Viemeister and Bacon (1982) did not observe an improvement of the absolute threshold following band-rejected stimuli.

6. Enhancement and physiology

The results of our experiments strongly suggest that the uninfluenced threshold in quiet is slightly elevated above the physical limits of the system. Two different mechanisms to produce this desensitization are conceivable – mechanical lateral suppression and neuronal lateral inhibition. Both these mechanisms could be active in physical quiet. In the following two paragraphs we will discuss possible implications of the mechanisms on the observed effect.

From two-tone physiological experiments it is known that strong mechanical suppression exists in the cochlea (Sellick and Russell, 1979). Active outer hair cell mechanisms, namely a lateral suppression of adjacent loci in the cochlea (Zwicker, 1986a,b), are thought to be responsible for this effect. It is possible that outer hair cells are mechanically active in quiet which may result in excitation as indicated by SOAEs or in mechanical suppression. The results of our experiment on the interference between band-rejected noise and SOAEs are a first indication that the process underlying the threshold improvement is not related to the fast mechanical amplification provided by outer hair cells which probably contributes to the generation of SOAEs. In addition, low-frequency tones can change the effectiveness of cochlear mechanics periodically (Patuzzi, 1984), probably by biasing the position of the basilar membrane. In our experiments, however, neither the Zwicker tone nor the accompanying threshold improvement was influenced by low-frequency biasing tones. Moreover, no mechanical correlates of the Zwicker tone in terms of otoacoustic emissions were measurable. Since, in addition, no beats between the Zwicker tone and a faint pure-tone

Table 2
Influence on threshold improvement of a low-frequency pure-tone masker presented simultaneously to the 4 kHz test signal

Simultaneously present low-frequency masker (45 Hz, 100 dB SPL)	Threshold shift versus threshold without preceding band-rejected noise (dB)	Standard error (dB)
No	−3.9	±0.5
Yes	−4.2	±0.3

The auditory threshold improvement was not significantly influenced by a low-frequency biasing tone. All other parameters like in Fig. 1.

stimulus of similar frequency can be found (Krump, 1993), our experiments render it unlikely that the threshold improvement and the Zwicker tone are mechanically produced at the level of the cochlea.

It is a much more promising alternative to assume a neuronal spectral processing to account for the present data. Palmer et al. (1995) made physiological recordings in the guinea pig from auditory nerve fibers excited by harmonic complexes with and without a spectral gap. No significant increase in average response rate caused by the signal component was found when the harmonic complex was preceded by the complex with the signal and adjacent harmonics missing relative to the response to the signal component without preceding stimulus. Thus, with the stimuli used in this experiment, auditory enhancement was absent in the auditory nerve.

Inhibitory interaction across frequencies is a compelling prerequisite for a neuronal circuit that could be responsible for our results. In the dorsal cochlear nucleus (DCN) neurons are found with very complex tuning curves, unlike the primary-like responses of ventral cochlear nucleus units (Young et al., 1992). The shape of these DCN tuning curves can be explained by inhibitory interaction of different cell types in the DCN. Young et al. found that some of the units are sensitive to notched noise. Nelken and Young (1995) suggested that the DCN might play an important role in the detection of interesting spectral features in broadband stimuli and that the DCN projection to the VCN might lead to a change in the spectral representation in the VCN that Nelken and Young called a 'whitening' of the spectral representation. The projection inhibits frequency regions outside a spectral notch more strongly than regions within the notch and thus leads to a compression of the spectral contrast in the VCN. Such a mechanism may provide a physiological correlate to auditory signal enhancement in the frequency range of a spectral notch.

7. Shifts in absolute threshold and auditory enhancement

Interpreted in the context of the auditory enhancement experiments briefly described in Section 1, our results imply a relationship between the Zwicker tone and enhancement effects: both of them are negative afterimages of the evoking stimulus (a broadband stimulus with a spectral gap). The Zwicker tone is the negative afterimage perceived in quiet and enhancement is the afterimage emerging on an acoustical background (i.e., a spectrally flat noise or complete harmonic spectrum). The results of Viemeister's and Bacon's forward-masking experiments of enhanced components, described in detail in Section 1, and our results, show that both these afterimages are accompanied by a true signal gain in the spectral region where the evoking stimulus contains no acoustic energy. On the other hand, it must be kept in mind that the conditions that have to be met to generate a Zwicker tone are stronger than those for producing auditory enhancement, but all band-rejected stimuli that lead to a Zwicker tone sensation generate auditory enhancement.

Viemeister and Bacon (1982) suggested that adaptation of a suppressive influence coming from the frequency regions outside the spectral gap into the region inside the gap could be the reason for the observed signal gain. Wright et al. (1993) evaluated the relation between the amount of psychophysical two-tone suppression and the amount of signal and masker enhancement in the same 6 subjects. The subjects showing the largest two-tone suppression showed the smallest amount of auditory enhancement and vice versa. These results questioned Viemeister and Bacon's conclusion that suppression may adapt. The reason for the inverse relationship between auditory enhancement and psychophysical two-tone suppression cannot be explained based on our findings. It may be hypothesized that the contradictory results are related to the different optimal stimulus combinations found for the two psychophysical paradigms. In psychophysical two-tone suppression, the largest suppression is found at a frequency relation of 1.15 (e.g., Shannon, 1976) between the suppressor and the masker. In auditory enhancement experiments, the amount of enhancement primarily depends on frequency components above 1.2 times the signal frequency (Wright, 1995).

Our results support Viemeister's primary conclusion that the internal representation of the signal is enhanced in auditory enhancement experiments. We were able to show the existence of a true signal gain also in quiet resulting in a temporary threshold improvement. Our observation concerning otoacoustic emissions and the low-frequency experiment lead us to suggest that the observed effects cannot be attributed to a release from mechanical suppression in the cochlea, but rather to a release from neuronal lateral inhibition in the cochlear nucleus or in higher monaural stations of the ascending auditory pathway.

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