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An auditory negative after-image as a human model of tinnitus

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Abstract

The Zwicker tone (ZT) is an auditory after-image, i.e. a tonal sensation that occurs following the presentation of notched noise. In the present study, the hypothesis that neural lateral inhibition is involved in the generation of this auditory illusion was investigated in humans through differences in perceptual detection thresholds measured following broadband noise, notched noise, and low-pass noise stimulation. The detection thresholds were measured using probe tones at several frequencies, within as well as outside the suppressed frequency range of the notched noise, and below as well as above the corner frequency of the low-pass noise. Thresholds measured after broadband noise using a sequence of four 130-ms probe tones (with a 130-ms inter-burst interval) proved to be significantly smaller that those measured using the same probe tones after notched noise at frequencies falling within the notch, but larger for frequencies on the outer edges of the noise. Thresholds measured following low-pass noise using the same sequence of probe tones were found to be smaller at frequencies slightly above the corner, but larger at lower, neighboring frequencies. This pattern of results is consistent with the hypothesis that the changes in auditory sensitivity induced by stimuli containing sharp spectral contrasts reflect lateral inhibition processes in the auditory system. The potential implications of these findings for the understanding of the mechanisms underlying the generation of auditory illusions like the ZT or tinnitus are discussed.

Key words: Zwicker tone; Auditory illusion; Negative after-image; Lateral inhibition; Tinnitus

1. Introduction

The Zwicker tone (ZT) is a transient auditory sensation which can be heard for a few seconds following stimulation of the ear by a notched noise, i.e. broadband noise containing a suppressed frequency band (Zwicker, 1964). It is an auditory illusion, in the sense that it does not correspond to any currently present stimulus in the environment. Zwicker (1964) characterized the most important characteristics of this sensation and of the stimuli required to induce it. The main results of his investigation can be summarized as follows. Firstly, the subjective perception is similar to that induced by a sinusoidal tone, with a pitch within the suppressed frequency range of the notch noise. Secondly, the pitch of the ZT increases with the level of the inducer. Thirdly, the ZT can be obtained with notch noise containing suppressed bands one half octave wide for center frequencies between 700 Hz and 6 kHz. Fourthly, the duration of the ZT increases with the duration of the inducer. Finally, a continuous ZT sensation can be induced by presenting 100-ms notched noise bursts at a repetition rate of about 5 Hz.

As recently pointed out by Hoke et al. (1996, 1998), the ZT may be used in order to try and gain further insight into the mechanisms underlying the generation of phantom auditory sensations like tinnitus in humans. The fact that it can easily be induced in normal-hearing subjects using moderate stimulus levels, and that it is entirely reversible, makes it a potentially very interest-

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Abbreviations: ZT, Zwicker tone; MEG, magnetoencephalography; 2I-2AFC, 2-interval 2-alternative forced choice; CF, characteristic frequency

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ing human model of tinnitus. In order to gain further insights into the neural substrate of the ZT phenomenon, these authors carried out magnetoencephalographic (MEG) recordings in normal-hearing subjects while they were hearing a ZT following notched noise stimulation (Hoke et al., 1996, 1998). The results indicated that the cortical region activated during the ZT sensation was similar to that activated by a tone of the same frequency. The authors concluded that the mechanisms underlying the ZT were similar to those involved in the perception of an external tone. In other words, the ZT appears likely to result from the brain mistaking an aberrant neural signal for a 'real' sound.

However, several questions regarding the underlying mechanisms responsible for the generation of the ZT remain unanswered. In particular, how does a fairly large (one half octave) notch in an otherwise flat noise induce a fairly sharp, tonal sensation? Pieces of information concerning the state of neural auditory centers following stimulation with spectrally notched sound have very recently been provided in a study by Pantev et al. (1999). Using MEG, these authors demonstrated that after prolonged stimulation with notched music, auditory cortex neurons responding to frequencies falling within the notch were strongly inhibited. The authors interpreted this result as reflecting the lasting effect of neural inhibitory processes, i.e. the inhibitory influence of the neurons that were stimulated onto the activity of the neighboring neurons that had characteristic frequencies (CFs) within the notched area. Lateral inhibition is commonly invoked as a mechanism responsible for the enhancement of contrasts between the activity of neighboring units in neural arrays or maps (Rhode and Greenberg, 1994). When applied recurrently, lateral inhibition leads to extreme activity states in which only a few units have a very large activity level while the others are strongly inhibited. This neural process may explain how fairly wide spectral contrasts in auditory stimuli result in very localized increases or decreases in neural activity in the central auditory system, which may be the neural substrate of tonal sensations like the ZT. Another aspect of the results of Pantev et al. (1999), which is consistent with lateral inhibition, consists of the observation that the activity of neurons with CFs corresponding to the edges of the spectral notch tended to be increased after stimulation following prolonged stimulation with notched music.

It is important to note that the observation and interpretation of Pantev et al. (1999) appear to be discrepant with those of Hoke et al. (1996) in the sense that whereas the former indicate that a notched stimulus induces a relative decrease in the activity of cortical auditory neurons which respond to the center of the notch, the latter indicate a relative increase in the activity of these neurons. Based on current knowledge, one can only speculate on the possible reasons for this discrepancy. First of all, it is important to remark that the underlying neural mechanism of the ZT in Hoke et al.'s study – namely, the relative increase in the activity of neurons responding to frequencies corresponding to the perceived pitch of the ZT – was not directly observed, but was inferred from the observation that the N1-off traces recorded in the presence of the ZT sensation are similar to those recorded in the presence of an external tone of corresponding frequency. On the other hand, Pantev et al. (1999) directly observed a decrease in the evoked activity of neurons which respond to frequencies corresponding to the notch. The two studies used different notched stimulus durations, but it is very unlikely that this methodological difference accounts for the finding of opposite results. Further studies are necessary to resolve the apparent paradox between the results of Hoke et al. (1996) and those of Pantev et al. (1999).

The general aim of the present study was to test the hypothesis that lateral inhibition processes are involved in the generation of the ZT. To this aim, we used a psychophysical approach inspired from an earlier study by Wiegrebe et al. (1996). In this study, the authors compared perceptual detection thresholds following a broadband noise, which contained a one half octave wide notch and induced a ZT, to thresholds obtained following spectrally flat noise, or in the absence of any inducer. Their results demonstrated that probe tones which followed the notched noise could be more easily detected than tones following spectrally flat noise or even no inducer, which ruled out forward masking as a possible explanation. These auditory enhancement effects were found to be largest around the center frequency of the notch, which corresponded to the perceived frequency of the ZT. These results indicate that the changes in neural responsiveness induced by notched noise stimulation are reflected at the behavioral level by changes in the detection thresholds. The decrease in the neural responsiveness of neurons with CF in the notch after the presentation of a spectrally notched stimulus reported by Pantev et al. (1999) thus corresponds to an increase in detection threshold.

Here, we further reasoned that if lateral inhibition processes operating on the neural pattern of activity induced in the auditory system by notched noise actually subtend the generation of the ZT sensation, one should expect not only reductions in detection thresholds close to the notch center frequency but also increases near the notch edges. Consequently, we carried out a first experiment in which we tested for changes in thresholds induced by notched noise at several probe frequencies falling within as well as outside the notch and around the notch edge frequencies.

In order to obtain further information as to the relationship between the ZT and the changes in absolute thresholds induced by notched noise in this experiment, we took advantage of the informal observation, made during the course of pilot experiments, that the diotic presentation of a notch noise generally resulted in a monaural ZT sensation. Namely, we tested whether the threshold enhancement effect occurred specifically in the ear in which the ZT was perceived when a binaural notched noise inducer was used.

In an attempt to test further the possible existence of relationships between the mechanisms responsible for the generation of ZT and those responsible for the generation of tinnitus, we carried out a second experiment in which the inducer consisted of low-pass noise instead of notched noise. Several authors have suggested that tinnitus, which is often accompanied by hearing loss (Sirimanna et al., 1996; Henry et al., 1999), may be related to functional deafferentation due to peripheral damages (Gerken, 1996; Salvi et al., 1995; Norena et al., 1999; Kimura and Eggermont, 1999; Kral and Majernik, 1996; Langner and Wallhäusser-Franke, 1999). As suggested by Pantev et al. (1999), the remanent effects of the inducers can be conceived as a 'reversible functional deafferentation'. While in normal-hearing subjects spectrally notched sound stimulation mimics the type of functional deafferentation corresponding to focal hearing losses, low-pass noise may be used to mimic the type of functional deafferentation corresponding to the kind of hearing loss which is most commonly observed in tinnitus sufferers, namely increased thresholds toward higher frequencies (Meikle et al., 1991; Henry et al., 1999). Interestingly, low-pass noise has been shown to elicit auditory after-images (Rosenblith et al., 1947). This second experiment thus aimed to test whether low-pass noise can, like notched noise, induce changes in the perceptual detection thresholds of probe tones following its presentation.

Table 1
Probe frequencies tested in the 10 subjects of experiment 1 (effect of a notched noise on absolute thresholds)

Subject	Test frequencies (kHz)								
1	2.8	3	3.2	3.8	4	4.4	5	5.2	5.4
2	–	3	–	–	4	–	–	–	–
3	–	3	–	–	4	–	–	–	–
4	–	3	–	–	4	–	–	5.2	–
5	–	3	3.2	–	4	–	–	5.2	–
6	2.8	3	3.2	3.8	–	4.4	5	5.2	5.4
7	2.8	–	3.2	3.8	4	4.4	5	5.2	5.4
8	2.8	3	3.2	3.8	4	4.4	5	5.2	5.4
9	2.8	3	3.2	3.8	–	4.4	5	5.2	5.4
10	–	3	3.2	–	4	–	–	5.2	–

2. Methods

2.1. Subjects

Ten subjects (five male, five female) between 20 and 30 years (mean = 25.6, S.E.M. = 0.65) took part in the measurement of absolute thresholds following the monaural presentation of broadband or notched noise in experiment 1. Five subjects (three male, two female) aged between 25 and 50 years (mean = 31.6; S.E.M. = 4.7) participated in a second part of the experiment, in which the inducers were presented diotically. These subjects were asked to report whether they heard the ZT sensation binaurally or monaurally, and if the latter, in which ear.

Experiment 2, in which absolute thresholds were measured following the monaural presentation of low-pass noise, involved six subjects (two male, four female) between 20 and 27 years (mean = 21.5; S.E.M. = 1.15). Due to the relatively long duration of the tests, not all probe frequencies could be tested in all the subjects. The frequencies tested in each subject are indicated in Tables 1 and 2. The ear tested (left or right) was chosen randomly in each subject.

All the subjects had normal hearing, i.e. absolute auditory thresholds within 20 dB HL between 500 and 8000 Hz at octaves, as measured using pure tone audiometry.

2.2. Stimuli

The stimuli used in this study consisted of bursts of broadband noise (control), band-rejected noise, low-pass noise, and tone bursts. The noise bursts were 1 s long and their overall level was set to 40 dB SPL. They were obtained by convolving a burst of gaussian noise with the impulse response of a rectangular filter computed by inverse digital fast Fourier transform; the spectral slopes of the noise on the borders of the notch were thus virtually infinite. The low and high corner frequencies of the rectangular filter were set to 3400 and 4800 Hz (i.e. roughly half an octave around 4 kHz). The low-pass noise was obtained from the notched noise after removal of the high-frequency

Table 2
Probe frequencies tested in the six subjects of experiment 2 (effect of a low-pass noise on absolute thresholds)

Subject	Test frequencies (kHz)						
C1	3	3.2	3.4	3.6	3.8	4	4.4
C2	3	3.2	3.4	–	3.8	4	4.4
C3	3	3.2	3.4	–	3.8	4	4.4
C4	3	3.2	3.4	3.6	3.8	4	–
C5	–	3.2	3.4	–	3.8	4	4.4
C6	3	3.2	3.4	3.6	3.8	4	–

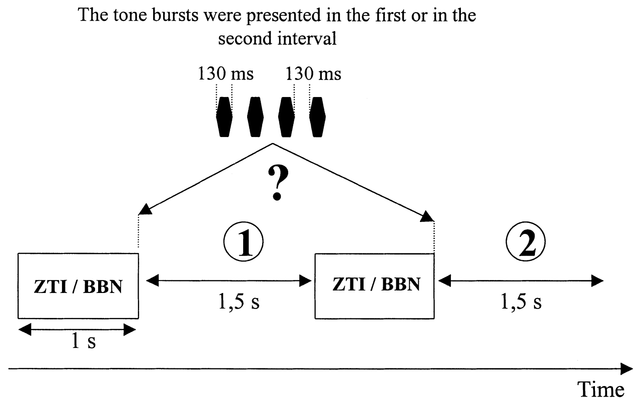

Fig. 1. Temporal sequence of stimuli. ZTI: Zwicker tone inducer (notched noise or low-pass noise); BBN: broadband noise (control condition). The subject's task was to indicate if the four tone bursts were in the first or the second interval.

band; thus, its corner frequency was at 3400 Hz. The signal to be detected by the subjects consisted of a sequence of four tone bursts, 130 ms long each (including 20 ms long cosine ramps), and separated by 130 ms long silent gaps. The sequence of tone bursts started immediately after the offset of the noise burst. Fig. 1 shows the temporal stimulation sequence.

Stimuli were played out using a 16-bit digital-to-analog converter at a sampling rate of 40 kHz using a Tucker Davis Technologies (TDT) system. They were low-pass filtered using an anti-aliasing filter (TDT FT6-2) with a 15-kHz corner frequency. They were then attenuated (TDT PA4), mixed (TDT SM3) and fed to Sennheiser HD465 headphones via a headphone buffer (TDT HB6). Stimulus calibration was checked using a Bruel and Kjaer (B&K) 4153 artificial ear with a B&K microphone connected to a B&K pre-amplifier and B&K 2636 measuring amplifier, fed to a HP 3561A dynamic signal analyzer. The notch depth was about 45 dB.

2.3. Psychophysical measures

Absolute thresholds corresponding to 70.7% correct detection were measured using a two-interval, two-alternative, forced choice (2I-2AFC) procedure with a two-down, one-up adaptive tracking rule[1]. Each interval contained a burst of broadband noise (control condition), notched noise, or low-pass noise. In one interval, chosen pseudo-randomly on each trial, the burst was immediately followed by a sequence of probe tones – as described above. The subjects' task was to indicate if the probe tones were present in the first or in the second interval. The initial step size, 3 dB, was reduced to 1 dB after the fourth reversal in signal level. The procedure stopped after 12 reversals. The threshold was computed as the average signal level over the last eight reversals. The subjects performed at least three runs. The thresholds shown in the figures were obtained by averaging the estimates across the different runs.

The effects induced by notched or low-pass noise were quantified by comparing thresholds measured following such inducers to those measured following broadband noise. We reasoned that comparison with a silent – i.e. unmasked – condition would be less relevant since the threshold differences could be biased by the fact that in the absence of inducer, the temporal intervals in the 2I-2AFC task would have to be marked by visual cues; listeners would thus rely on visual cues in this condition, but could ignore these visual cues in the other conditions in which both intervals were acoustically marked. Therefore, we chose not to include a silent condition, and not to mark the auditory intervals with visual cues.

3. Results

Figs. 2 and 3 represent the differences between absolute thresholds measured following monaural broadband and notched noise. Negative differences indicate

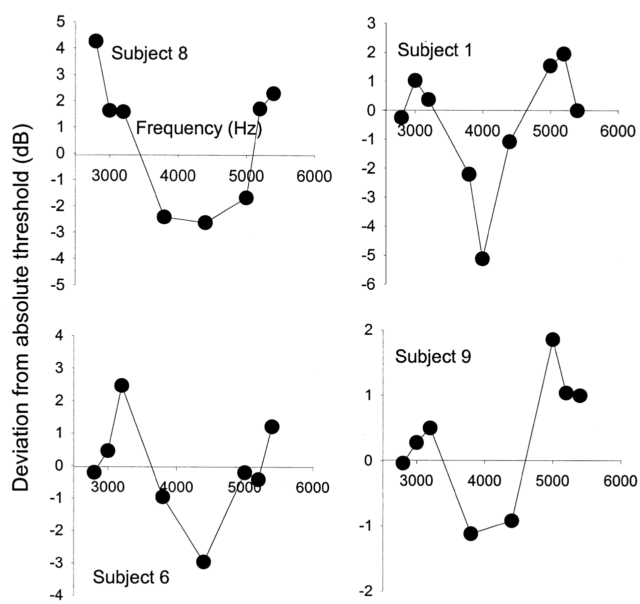

Fig. 2. Differences in the detection thresholds of probe tones following broadband noise versus notched noise in four subjects. Negative differences indicate smaller thresholds for notched than for broadband noise; positive differences indicate larger thresholds for notched than for broadband noise.

[1] A two-interval forced choice procedure was preferred over a yes/no procedure because threshold estimates are less likely to be contaminated by false alarms resulting from confusion between the ZT and the signal in the notched noise condition using a fixed criterion procedure.

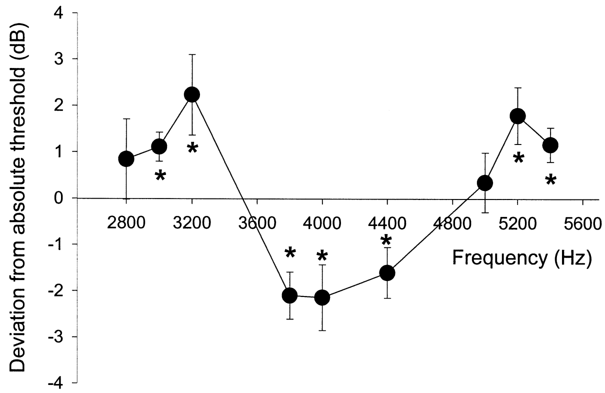

Fig. 3. Differences in the detection thresholds of probe tones following broadband noise versus notched noise averaged across all subjects ($n = 10$). Negative differences indicate smaller thresholds for notched than for broadband noise; positive differences indicate larger thresholds for notched than for broadband noise (*$P < 0.05$, paired t-test).

smaller – i.e. improved – thresholds following notched than broadband noise; positive differences correspond to larger – i.e. worsened – thresholds for notched noise. The statistical significance of the results was tested using paired Student's t-tests. The results revealed that thresholds were significantly lower – i.e. improved – for notched than for broadband noise at frequencies within the spectral gap – namely, at 3800, 4000 and 4400 Hz ($P < 0.05$). In contrast, the absolute thresholds were significantly higher at frequencies corresponding to or just below the notch corners – namely, at 3000 and 3200 Hz on the low-frequency side, and 5200 and 5400 Hz on the high-frequency side of the notch ($P < 0.05$).

The differences in absolute thresholds induced by diotic notched noise are shown in Fig. 4. The results of a questionnaire in which the subjects had to indicate

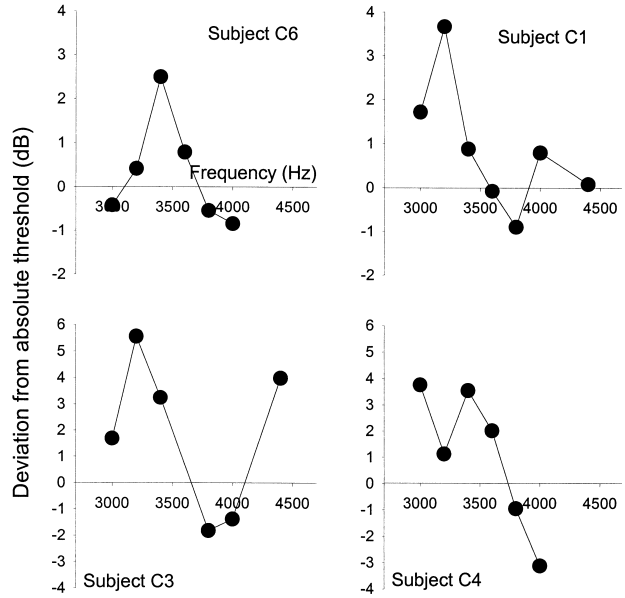

Fig. 5. Differences in the detection thresholds of probe tones following broadband noise versus low-pass noise in four subjects. Negative differences indicate smaller thresholds for notched than for broadband noise; positive differences indicate larger thresholds for notched than for broadband noise.

whether the ZT was heard in the right, the left, or both ears revealed that the ZT elicited by the presentation of diotic notched noise was systematically heard monaurally. Although the ear in which the ZT was heard varied across subjects, it was always the same on different presentations of the diotic noise in a given subject. Sixty percent of the subjects had their ZT in the left ear; the remaining 40% had it in the right ear. The results of paired t-tests indicated that thresholds were significantly lower after diotic notch noise than after

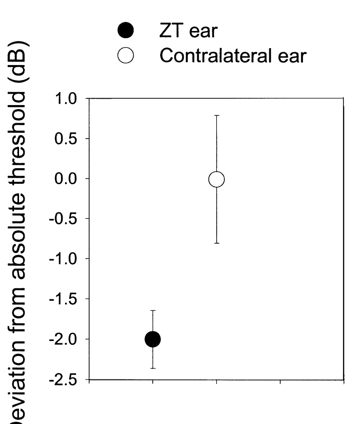

Fig. 4. Differences in the detection thresholds of probe tones following diotic broadband noise versus diotic notched noise in four subjects. Negative differences indicate smaller thresholds for notched than for broadband noise.

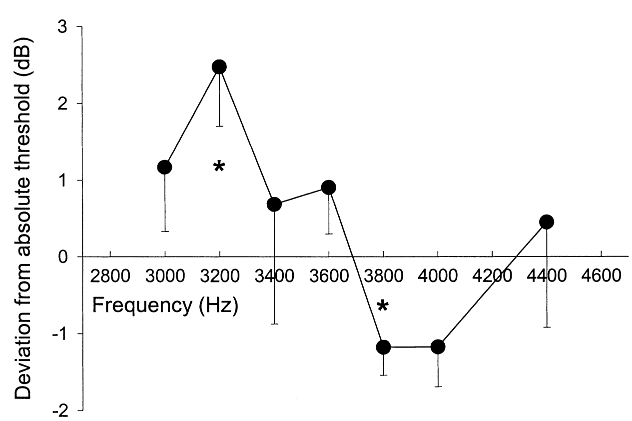

Fig. 6. Differences in the detection thresholds of probe tones following broadband noise versus low-pass noise averaged across all subjects ($n = 6$). Negative differences indicate smaller thresholds for notched than for broadband noise; positive differences indicate larger thresholds for notched than for broadband noise (*$P < 0.05$, paired t-test).

diotic broadband noise stimulation in the ear in which the ZT was heard ($P < 0.01$), but not in the opposite ear ($P > 0.05$).

Figs. 5 and 6 show the results of experiment 2 in which differences in absolute thresholds induced by monaural low-pass noise, as compared to broadband noise, were measured. Negative differences indicate smaller – i.e. improved – thresholds following low-pass than broadband noise while positive differences indicate larger – i.e. worsened – thresholds. The paired *t*-tests indicated that thresholds were significantly improved at 3800 Hz ($P < 0.05$), i.e. above the low-pass noise corner frequency, and impaired at 3200 Hz ($P < 0.05$), i.e. below the low-pass noise corner.

When comparing visually the results obtained in the notched noise and low-pass noise conditions, a trend for the threshold improvement effects to be larger in the former than in the latter condition can be noted. However, this difference proved not to be statistically significant ($t = 0.997$, $P = 0.34$ at 4 kHz).

4. Discussion

The present results are consistent with earlier data from Wiegrebe et al. (1996) in showing that absolute thresholds following notched noise are significantly smaller than following broadband noise at frequencies close to the notch center. The difference between the notched and broadband noise conditions which these authors measured using a 2I-2AFC procedure (6.9 dB at 4 kHz on average in four subjects) was larger than that observed here (about 2.2 dB at the same frequency on average in eight subjects). This difference is unlikely to result from the minor procedural differences between the two studies – namely, the use of a three-down, one-up tracking rule converging toward 79% correct responses in Wiegrebe et al. (1996) versus the use of a two-down, one-up tracking rule converging toward 70.7% correct here. Although the stimuli used in the two studies had the same gross temporal and spectral characteristics, it is conceivable that subtle differences in the spectral characteristics of the noise used in Wiegrebe et al.'s study and that used here were responsible for the observed difference. In particular, Wiegrebe et al. (1996) equalized the spectral level of the noise, which we did not. Finally, another possible explanation for the observed difference between the two studies comes from inter-individual variability. Whatever caused this difference in the size of the effects obtained at frequencies within the notch region, an important point is that these effects were of the same sign in the two studies, indicating better sensitivity following notched than broadband noise.

A new finding of the present study corresponds to the finding that absolute thresholds are significantly larger following notched than broadband noise at probe frequencies close to the corner frequencies of the notch. Although Wiegrebe et al. (1996) did not mention any difference between thresholds measured after notched and broadband noise at probe frequencies outside the notch, a 1.5-dB average threshold increase can be seen in the data of their three listeners tested at 3 kHz. This is in agreement with the results averaged across the nine subjects tested at 3 kHz in the present study. The data from the current study reveal an even larger degradation in detection thresholds at 3.2 kHz, a frequency nearer to the corner frequency of the notch. Interestingly, for low-pass noise, thresholds also proved to be significantly larger than following broadband noise for this 3200 Hz probe frequency, while they were significantly smaller for the 3800-Hz probe frequency, well above the noise corner frequency.

Wiegrebe et al. (1996) have argued that the difference in absolute thresholds observed after notched and broadband noise stimulation cannot be accounted for simply in terms of forward masking since, firstly, the time course of forward masking is shorter than the duration of the probe tone sequence, and, secondly, thresholds measured after notched noise are smaller even when compared to a silent – i.e. no inducer – condition; this suggests a genuine enhancement of auditory sensitivity. The present results add further support to the view that the thresholds changes do not reflect forward masking since, as observed using probe frequencies located near the notch edges, they can be *larger* following notched noise than following broadband noise – whereas forward masking effects should in no case be smaller for broadband noise than for notched noise.

The neurophysiological mechanisms underlying the ZT and the changes in hearing sensitivity that accompany it are unclear. Wiegrebe et al. (1996) investigated the possible role of cochlear mechanisms in these phenomena. They found that although the perceived intensity of a spontaneous otoacoustic emission was increased after the presentation of a noise having a notch centered on the spontaneous otoacoustic emission frequency, the amplitude of the spontaneous otoacoustic emission remained unchanged. Furthermore, neither the perception of the ZT nor the threshold enhancement effect was significantly influenced by a simultaneous, low-frequency tone pip introduced to bias the cochlear mechanics. The authors concluded that the ZT and the auditory enhancement phenomena were very unlikely to have their origin at the level of the cochlea. Physiological recordings by Palmer et al. (1995) further suggest that the auditory enhancement effect is not present at the level of the auditory nerve and must be sought in the upper stages of the auditory system.

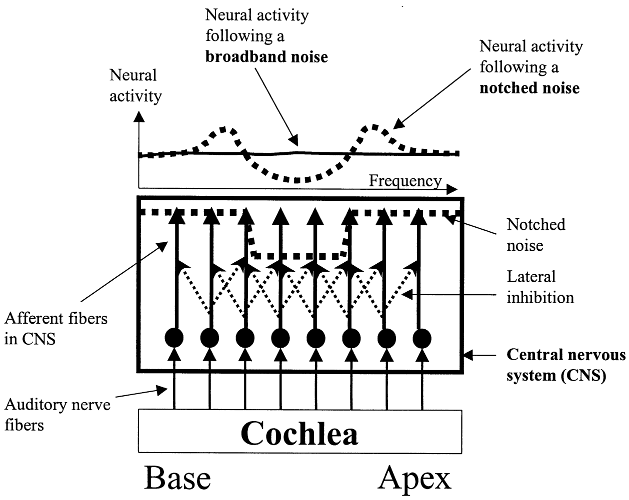

Fig. 7. Highly simplified schematic of peripheral and central auditory processes which may explain the generation of the ZT and the threshold changes induced by broadband noise versus notched or low-pass noises.

Most neurons in the central auditory system do not only receive excitatory inputs from lower stages and from neighboring units; they also receive lateral inhibitory connections (Evans and Zhao, 1993; Rhode and Greenberg, 1994). These lateral inhibitory connections are commonly thought to play a crucial role in the processing of auditory information. In particular, they contribute to enhancing spectral contrasts in the stimulus, which often bear important information (Rhode and Greenberg, 1994). Lateral inhibition has been proposed to play a role in the generation of phantom auditory sensations like tinnitus (Gerken, 1996; Salvi et al., 1995; Kimura and Eggermont, 1999; Norena et al., 1999; Kral and Majernik, 1996; Langner and Wallhäusser-Franke, 1999) or the ZT (Wiegrebe et al., 1996). The patterns of results evidenced in experiment 1 – i.e. positive threshold differences between the notched and broadband noise inducers for probe frequencies falling within the notch, negative differences on the borders of the notch, and no effect at remote frequencies – and experiment 2 – i.e. positive threshold differences below the corner frequency of low-pass noise, and negative differences above – are consistent with the operation of lateral inhibition processes in the central auditory system (Fig. 7).

An interpretation of our results in terms of lateral inhibition is also consistent with recent results from Pantev et al. (1999) regarding the effect of 'notched' music on the activity of the human auditory cortex. In that study, subjects listened for 3 h to pieces of music from which a narrow frequency band centered on 1 kHz had been removed. Immediately after listening to this notched music, MEG recordings revealed that the cortical source for a 1-kHz test stimulus – falling inside the 'functionally deafferented part' – was significantly decreased, while it was non-significantly increased for a 0.5-kHz control stimulus – falling outside the 'functionally deafferented part'. The authors suggested that changes in the efficacy of lateral connections – i.e. the unmasking of lateral connections produced by the 'functional deafferentation' – could explain this short-term plasticity effect.

The psychophysical results obtained in the present study may reflect a similar rapid remodelling of lateral connections in the central auditory system; further details on the underlying mechanism are provided in Fig. 7. Fig. 7 shows a highly simplified schematic of peripheral and central auditory processes which may explain the generation of the ZT and the threshold changes induced by broadband noise versus notched or low-pass noises. The activity of neurons with CFs located far away from the notch edges is determined by their excitatory inputs plus the inhibitory influence – lateral inhibition – which they receive from neighboring units. The spectral contrast which corresponds to the notch causes an imbalance in this pattern of excitation and inhibition. Namely, units whose CFs are located close to the notch edges – but still outside the notch – receive less inhibitory influence from neighboring units because some of these units have CFs located inside the notch and are thus not excited. Consequently, the activity of these neurons with CFs close to the notch cutoff frequencies is increased (Fig. 7). Conversely, these same neurons exert an inhibitory influence on neurons whose CFs fall within the notch region. Given that the latter are not excited, their activity is strongly suppressed (Fig. 7).

Furthermore, the fact that the threshold tended to rise again – impairment – as the probe frequency was increased above the low-pass noise cutoff (subjects C1 and C3) is noteworthy. It is conceivable that the inhibition of neural activity close to the noise cutoff frequency, which was caused by the suppressing influence of the neighboring units with lower CFs which were excited by the noise, in turn caused a release from inhibition of neighboring units having higher CFs. The fact that this effect shows up in certain listeners but not others might stem from variation in the spatial extent of inhibitory connections across subjects (i.e. microanatomical variability).

A secondary outcome of the present study which deserves mention corresponds to the fact that when the notched noise inducer was presented diotically, the ZT sensation was perceived in one ear rather than in both ears or in the middle of the head. Furthermore, a significant difference between notched and broadband noise was only observed on the perceived side of the ZT. The finding that dichotic noise induces a monaural ZT sensation and larger threshold variations in one ear than in the other is surprising. In an earlier study (Krump, 1993), it was found that the presentation of diotic notched noise induced a ZT sensation in the middle of the head. This apparent discrepancy between the present and earlier results may reflect inter-individual variability. If this observation is confirmed in future studies, it might be worth considering a possible explanation in terms of inter-aural inhibition, with one ear being dominant, i.e. inhibiting the perception of the ZT in the other. In any event, this observation provides an additional argument for the existence of a relationship between the mechanisms responsible for the generation of the ZT and those underlying the changes in hearing thresholds following notched noise stimulation.

An important question is whether the short-term reversible remodelling of lateral inhibitory which presumably subtends the results of the present and earlier studies (Wiegrebe et al., 1996; Pantev et al., 1999) can also explain the generation of tinnitus, which, in contrast to the effects observed in those studies, appears to reflect a long-term, chronic change in the auditory system. A possible explanation is that in the case of tinnitus, a permanent contrast in the activity of auditory nerve fibers across frequency is imposed by cochlear damages. In a large majority of cases, subjects suffering from tinnitus have a hearing loss (Sirimanna et al., 1996; Henry et al., 1999; Meikle et al., 1991). Several observations indicate that following cochlear lesions affecting the inner hair cells, the activity of afferent neurons responding to lesioned frequencies is decreased as compared to that of units connected to intact portions of the cochlea (Kiang et al., 1970; Liberman and Dodds, 1984). Based on these observations, it has been proposed that cochlear damages induce a permanent spectral contrast in auditory system activity and that lateral inhibition, by enhancing such contrasts, may be responsible for the generation of tinnitus (Gerken, 1996). This model is consistent with the fact that in most cases, tinnitus manifests as a tonal sensation (Gabriels, 1995; Vernon and Press, 1995) with a pitch corresponding to a frequency located at or close to the frequency at which the hearing loss is the largest, or close to the corner frequency of the audiogram (Henry et al., 1999). The results of the present study, which demonstrate changes in hearing sensitivity across frequency following stimulation with notched and low-pass noise, provide further support for the notion that the ZT may prove to be a useful human model to study the conditions responsible for the generation of tinnitus.

Another important question, which future investigations will have to address, is whether phantom auditory sensations like the ZT and tinnitus correspond to a local increase, a decrease, or rather a contrast in neural activity. The results of Hoke et al. (1996, 1998) suggest that the ZT is represented by a relative locally increased neural activity at the cortical level. This finding can be paralleled with the hypothesis that tinnitus results from locally increased spontaneous activity in the auditory system (Jastreboff, 1990). However, it is at variance with the results from Pantev et al. (1999), which suggest that units responding to frequencies within the notch are strongly inhibited. A possible solution to this discrepancy lies in the fact that auditory illusions may in fact correspond to spectral contrasts, rather than maxima in the activity of tonotopically organized arrays of neurons in the central auditory system.

5. Conclusion

The results of the present study provide further insight into the mechanisms underlying the generation of tonal auditory illusions from spectral contrasts in peripheral auditory activity in humans. Specifically, they indicate an involvement of short-term functional changes in neural lateral inhibition processes in the generation of the ZT. While in the present study the spectral contrasts in peripheral auditory system activity over which the lateral inhibition mechanisms operated were induced by stimulation with notched or low-pass noise, in subjects with hearing loss, permanent spectral contrasts in peripheral auditory system activity may exist due to cochlear damages, and might explain the fact that tinnitus, contrary to the ZT, is not a reversible auditory illusion.

The results also provide further support for the notion that the changes in detection thresholds and the tonal illusion which occur following stimulation with a notched noise are related, since when the noise is diotic, the threshold change is obtained in the ear in which the ZT is perceived. However, further study is required in order to determine the extent to which the perceived location of the ZT varies across subjects.

The present results also suggest several questions worth investigating in future research work. In particular: does the neural substrate of transient and permanent auditory illusions like the ZT and tinnitus consist in local decreases in neural activity (Pantev et al., 1999), or more generally, in contrasts between the activity of neighboring units in tonotopically organized neural arrays rather than local increases as traditionally thought (Jastreboff, 1990)? What are the conditions necessary for lateral inhibition processes to lead to patterns of neural activity in the central nervous system which are perceived as sounds? The ZT illusion requires specific stimulation conditions to occur, especially regarding the width of the notch, which may relate to anatomical or functional constraints on the operation of lateral inhibitory connections in the auditory system. If tinnitus is underlain by the same lateral inhibition processes, one may expect it to occur only for certain patterns of cochlear damages.

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