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Simultaneous suppression of tone burst-evoked otoacoustic emissions – effect of level and presentation paradigm

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Abstract

There is conflict in the literature over whether individual frequency components of a transient-evoked otoacoustic emission (TEOAE) are generated within relatively independent "channels" along the basilar membrane (BM), or whether each component may be generated by widespread areas of the BM. Two previous studies on TEOAE suppression are consistent with generation within largely independent channels, but with a degree of interaction between nearby channels. However, both these studies reported significant suppression only at high stimulus levels, at which the "nonlinear" presentation paradigm was used. The present study clarifies the separate influences of stimulus level and presentation paradigm on this type of suppression. TEOAEs were recorded using stimulus tonebursts at 1, 2 and 3 kHz and a complex stimulus consisting of a digital addition of the three tonebursts, over a range of stimulus levels and both "linear" and "nonlinear" presentation paradigms. Responses to the individual tonebursts were combined offline and compared with responses to the complex stimuli. Results clearly demonstrate that TEOAE suppression under these conditions is dependent upon stimulus level, and not upon presentation paradigm. It is further argued that the data support the "local" rather than "widespread" model of TEOAE generation, subject to nonlinear interactions between nearby generation channels.

Introduction

Transient-evoked otoacoustic emissions (TEOAEs) in response to click stimuli are typically recorded as complex, multi-frequency responses. The bulk of available data to date indicate the existence of relatively independent "generator channels", in that individual frequency components within the response are relatively unaffected by the presence of stimulus or response components at other frequencies (e.g. Kemp, 1978; Probst *et al*, 1986; Xu *et al*, 1994; Prieve *et al*, 1996; Tavartkiladze *et al*, 1997; Ueda, 1999). Further, a given response component is thought to be evoked by a stimulus component at the same frequency, and presumably at the corresponding tonotopic location along the basilar membrane (BM) (Kemp, 1978; Elberling *et al*, 1985; Norton and Neely, 1987). These concepts may be described as representing a one-to-one relationship between stimulus and response frequency components, in the generation of TEOAEs.

Recent suggestions for classification of otoacoustic emissions, based on understanding of their generation mechanisms rather than measurement techniques (e.g. Shera, 2004), also suggest that TEOAEs are generated by pre-existing "place-fixed" mechanical perturbations in cochlear mechanics. Such suggestions are consistent with the local, relatively independent generation of TEOAE frequency components as described above.

Some authors have, however, reported contrary findings that suggest other models of TEOAE generation. For example, Sutton (1985) and Withnell and Yates (1998) reported that the suppression of a TEOAE by a pure tone is not restricted to the frequency region of the pure tone. Withnell and Yates (1998) also observed *enhancement* of TEOAE responses at frequencies lower than the "suppressor" tone frequency. Avan *et al* (1995, 1997) observed

changes in low frequency components of the TEOAE following damage to the basal region of the BM. Carvalho *et al* (2003) reported TEOAE phase data that suggested that a TEOAE "at frequency f cannot come from that place tuned to f". All of these findings suggest that the generators of individual TEOAE frequency components may in fact be distributed along the length of the BM. Most recently, Withnell and McKinley (2005) suggest that, at least in the guinea pig, relatively early TEOAE components are generated by a mechanism distributed along the BM, while relatively late components have local, "place-fixed" origins.

Other authors have obtained results that may be broadly consistent with the principle of local, independent generator channels, with, however, some interaction between such channels under certain conditions. Specifically, Xu et al (1994) and Yoshikawa et al (2000) found a degree of reduction or "suppression" of the response component at one frequency in the presence of a stimulus (and response) component that was 500 to 1,000 Hz higher. Xu et al (1994) found that the TEOAE in response to a 1 kHz tone burst was reduced in amplitude by the simultaneous presentation of a pair of tone bursts at 2 and 3 kHz. Similarly Yoshikawa et al (2000) reported varying levels of suppression of the response to a 1 kHz tone burst when simultaneously presenting a tone burst centred at either 1.5, 2 or 3 kHz. This suppression was greatest with the combination of 1 and 1.5 kHz tone bursts (i.e. smallest frequency separation).

One notable aspect of the findings of Xu et al (1994) and Yoshikawa et al (2000) was that the above suppression was only evident at high levels of stimulation – Xu et al (1994) reported suppression at stimulus levels of 75 dB p.e. (peak equivalent) SPL, but not at 37 dB p.e. SPL and 59 dB p.e. SPL, and Yoshikawa et al (2000) reported significant suppression at 70 dB p.e. SPL but not at 60 dB p.e. SPL. In both these studies, however, the responses at the highest

stimulus level (which exhibited suppression) were also obtained using the "nonlinear" presentation paradigm often used in TEOAE measurements (Kemp *et al*, 1990). In contrast, responses at the lower stimulus levels (which did not exhibit suppression) were obtained using the more simple "linear" presentation paradigm.

The nonlinear presentation paradigm cancels out linearly-scaling components in TEOAE recordings at two different stimulus levels, whilst partially preserving nonlinearly-scaling components. The technique is of great practical value in removing the (linear) "ringing" of the stimulus click that would otherwise obscure the early (high-frequency) component of the TEOAE. TEOAE responses themselves typically exhibit a compressively nonlinear inputoutput (I-O) function, and are therefore not cancelled by the nonlinear paradigm. However, they are somewhat reduced in amplitude relative to recordings that do not implement the paradigm ("linear recordings"). Of more relevance to the present study, the nonlinear presentation paradigm also complicates the interpretation of the suppression data obtained by Xu et al (1994) and Yoshikawa et al (2000). For example, in the case of the stimuli presented in the nonlinear paradigm at a nominal level of 75 dB p.e. SPL, the amount of suppression is dependent upon three variables – suppression at a true stimulus level of 75 dB p.e. SPL, suppression at a true level of 85 dB p.e. SPL and the nonlinear relationship between responses at 75 dB p.e SPL and 85 dB p.e. SPL governed by the compressive nonlinearity of the TEOAE I-O function. Additionally, while the results were held to show that suppression increases with stimulus level, the data of Xu et al (1994) indicate no significant suppression at either of the lower levels used, and a somewhat abrupt onset of suppression at the higher "nonlinear" level. Likewise Yoshikawa et al (2000) describe suppression increasing with level, it is only at the higher "nonlinear" level that the suppression is shown to be significant. These data therefore raise the question as to whether the salient difference between stimuli

that did or did not produce suppression was the presentation paradigm rather than the level of the stimulus.

The main aim of the present study was to determine whether the suppression of TEOAE responses as previously reported by Xu *et al* (1994) and Yoshikawa *et al* (2000) is entirely a function of stimulus level, or whether it is influenced by the presentation paradigm used. The secondary aim was to characterise any dependence of suppression upon stimulus level in greater detail than the previous work.

Materials and methods

Subjects

Subjects were fourteen normally hearing adults (10 female, 4 male), aged 21 to 28 years (median = 24.4 years). All subjects had audiometric thresholds of 15 dB HL or better from 0.25 to 8 kHz in the ear tested, and normal middle ear status as measured by otoscopic examination and tympanometry. TEOAEs in response to click stimuli were initially measured in both ears, and the ear with the larger TEOAE amplitude in each subject was selected for inclusion in the study. Eight right ears and six left ears were included.

Instrumentation and stimuli

Stimuli were generated and responses recorded using the Otodynamics ILO 88 system with software version 5.60. Two types of stimuli were generated using routines available in the ILO 88 software: a) simple cosine-windowed tone bursts of 5 ms duration (rise-fall time = 2.5 ms, plateau = 0 ms) with centre frequencies of 1, 2 and 3 kHz and b) a "complex" stimulus resulting from the digital addition of the three simple tone bursts. Stimuli were presented at approximately 55, 65, 70, 75, 80 and 85 dB p.e. SPL using the "linear presentation" paradigm of the ILO 88, i.e. conventional averaging. Stimuli at 65, 70 and 75 dB p.e. SPL were also presented using the ILO 88 "nonlinear presentation" paradigm. Stimuli in the nonlinear presentation paradigm were delivered in series of four tone-bursts, three at the same amplitude and polarity, and the fourth with an amplitude three times greater and inverted polarity (principle described by Kemp *et al*, 1990). Stimuli were presented at an inter-stimulus interval of 20.48 ms and two replicate ('A' and 'B' responses, which resulted from 260 averages each, were recorded. To check for any system nonlinearities that could produce artifactual "suppressive" effects, the acoustic waveforms of the simple and complex

tone-bursts in a passive cavity were recorded. Figure 1 shows an example of spectra resulting from the acoustic waveform of the complex stimulus and spectra resulting from the addition of the acoustic waveforms of the simple tone-bursts at 1, 2 and 3 kHz presented at 75 dB p.e. SPL. Spectral components of the stimuli were almost identical with no systematic differences.

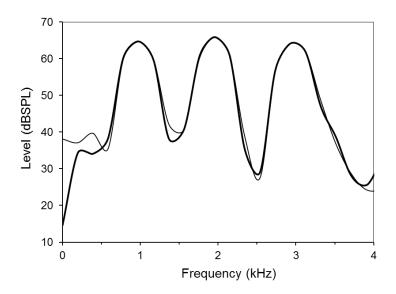


Figure 1. Spectra resulting from the acoustic waveform of the complex stimulus (bold line) and the addition of the acoustic waveforms of the simple tone-bursts at 1, 2 and 3 kHz (fine line) presented at 75 dB p.e. SPL recorded in a passive cavity. Spectral components of the stimuli were almost identical with no systematic differences.

Procedure

All recording of TEOAEs took place in a sound-attenuated booth, with the subject comfortably seated in an arm-chair. The subject was asked to remain quiet and still. The ILO 88 probe was fitted and sealed into the ear canal with a foam tip and taped into position. Probe fit integrity was verified using the ILO 88 'checkfit' facility. Stimuli were presented in the following order: 1) 1 kHz tone burst, 2) 2 kHz tone burst, 3) 3 kHz tone burst and 4) complex tone burst.

Analysis

A mean response waveform was calculated for each simple tone burst centred at 1, 2 and 3 kHz and the complex stimulus. The mean response waveforms for the three simple tone bursts were then added together to generate a "composite" response waveform. Both the composite and the mean complex response waveforms were windowed off line between 8 ms and 20.44 ms using Hanning rise and fall segments of 2.52 ms in order to remove stimulus ringing from the waveform. This relatively late-onset time window was necessary in order to remove stimulus ringing from the waveform at stimulus levels greater than 70 dB p.e. SPL, at the cost, however, of the loss of a substantial proportion of the 3 kHz component of the response. As the main focus of the present work was on the suppression of the responses at 1 and 2 kHz, the loss of some of the 3 kHz response component was not considered to be material.

Signal and noise frequency spectra in dB SPL of the composite and complex response waveforms were calculated off line. (Signal spectra were calculated from the mean of the 'A' and 'B' replicate waveforms and noise spectra from the difference between these two waveforms.) These spectra were then scaled to match the "Response FFT" levels calculated by the ILO 88 software, to enable direct comparison with the previous studies, which utilised the spectra calculated by that software. All signal spectra were then clipped at the corresponding noise floors by replacing any values of the signal spectrum below the noise floor by the value of the noise spectrum at that frequency. All further spectral analyses were conducted using these clipped spectra. This ensured that any differences subsequently

¹ Preliminary analyses showed that for a given condition, waveforms in response to the complex stimuli contained the greatest noise levels. For this reason both composite and complex signal spectra were clipped using the corresponding complex noise spectra.

obtained between complex and composite spectra would have arisen from points in the spectra that were clear of the noise floor.

Both composite and complex spectra were divided into bands 240 Hz wide ranging from 480 Hz to 3840 Hz and the mean level within each band was calculated for all composite and complex spectra. This resulted in fourteen bands, denoted B1-B14, that could be used for comparison between composite and complex spectra for each level and condition. Within each of the fourteen bands, suppression is defined as the difference in spectral level between the composite and complex spectra. A significance level of p < 0.005 was used for subsequent statistical analysis to allow for multiple hypothesis testing.

Results

Figure 2 shows an example of the TEOAE response waveforms for tone bursts at 1, 2 and 3 kHz. Figure 3 shows the TEOAE replicate response waveforms in response to the corresponding complex stimulus for the same ear. Figure 4 shows the signal spectrum resulting from the addition of the responses shown in figure 2, i.e., the composite spectrum, and the signal spectrum of the response waveforms shown in figure 3, i.e., the complex spectrum. Both the composite and complex response spectra show broad peaks of energy that correspond to the frequencies of the stimulus tone bursts.

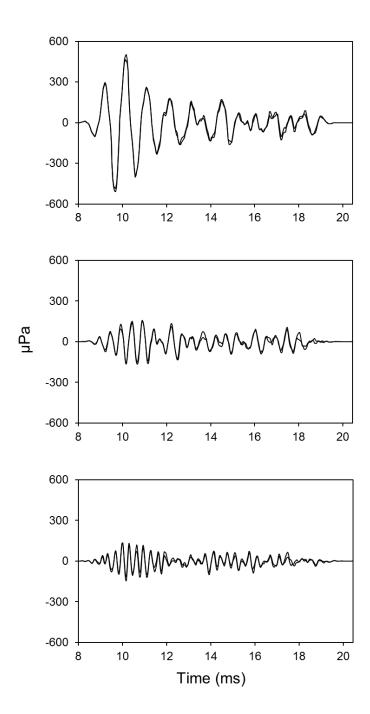


Figure 2. Example of replicate time waveforms ('A' and 'B') for responses to tone bursts centred at 1 kHz, 2 kHz and 3 kHz presented linearly at 65 dB p.e. SPL. Time waveforms were windowed between 8 ms and 20.44 ms using Hanning rise and fall segments of 2.52 ms.

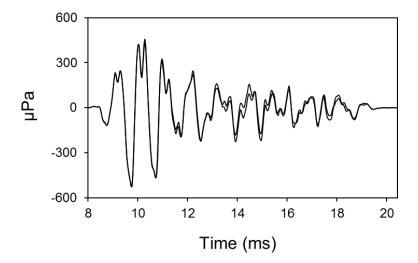


Figure 3. Replicate time waveforms ('A' and 'B') in response to the complex stimuli presented linearly at 65 dB p.e. SPL. Time waveforms were windowed between 8 ms and 20.44 ms using Hanning rise and fall segments of 2.52 ms.

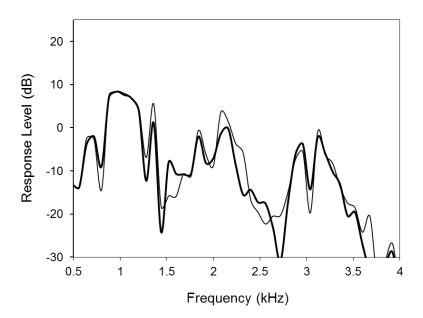


Figure 4. Composite spectrum resulting from addition of the mean of waveforms 'A' and 'B' for the 1, 2 and 3 kHz tone bursts shown in figure 2, and the spectrum of the mean of time waveforms 'A' and 'B' for the response to the corresponding complex stimuli shown in figure 3. The composite and complex response spectrum clearly shows broad peaks of energy that correspond to the frequencies of the stimulus tone bursts.

A comparison of the composite and complex spectra revealed a close correspondence within all ears. Figures 5 and 6 show example composite and complex spectra for two representative subjects, for each of the six stimulus levels used. Data from the linear presentation paradigm only are shown. The spectra exhibit the marked peaks and troughs typical of individual TEOAEs, but certain characteristics can be observed. Within each subject, peaks in the spectra occurred at the same frequencies, whether the stimulus was a single tone burst or the complex stimulus. However, small differences between the composite and complex spectra were observed for responses to stimuli at higher levels. These differences were reductions in the levels of the complex relative to the composite spectra (i.e. suppression), predominantly along the high-frequency slopes of the peaks at 1 kHz and 2 kHz. Figure 7 shows the mean composite and complex spectra for all ears, for each of the six stimulus levels used. Again, data from the linear presentation paradigm only are shown. The pattern of suppression as described above for individual subjects, and a tendency for the amount of suppression to increase with increasing stimulus level is clearly apparent. It can also be observed from figure 7 that while the peak at 3 kHz shows a tendency to become less prominent with increasing stimulus level, the peak at 1 kHz increases in level with increasing stimulus level.

Paired comparison t-tests of the spectral levels within individual bands for stimulus level presented using the linear paradigm were performed using a strict significance level (p < 0.005). Significant suppression was only observed across the high-frequency portion of the 1 and 2 kHz peaks in the complex spectra. Suppression of the high-frequency portion of the 3 kHz peak, although apparent in some panels in figure 7, was not statistically significant (p > 0.05). Further statistical analysis of the effect of paradigm and level on suppression was restricted to those bands shown to contain significant levels of suppression. These were B4

(1.20 – 1.44 kHz), B5 (1.44 – 1.68 kHz), B7 (1.92 – 2.16 kHz), B8 (2.16 – 2.40 kHz) and B9 (2.40 – 2.64 kHz).

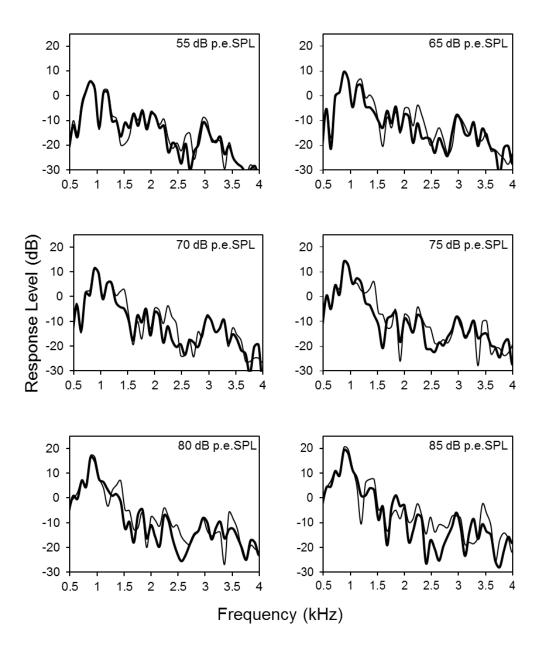


Figure 5. Spectra for complex (bold line) and composite (fine line) for linear presentation conditions for a representative subject. Although there is a close correspondence between the two spectra, reductions in the levels of the complex relative to the composite spectra (i.e. suppression), predominantly along the high-frequency slopes of the peaks at 1 kHz and 2 kHz can be observed. There is also a tendency for the suppression to increase with stimulus level.

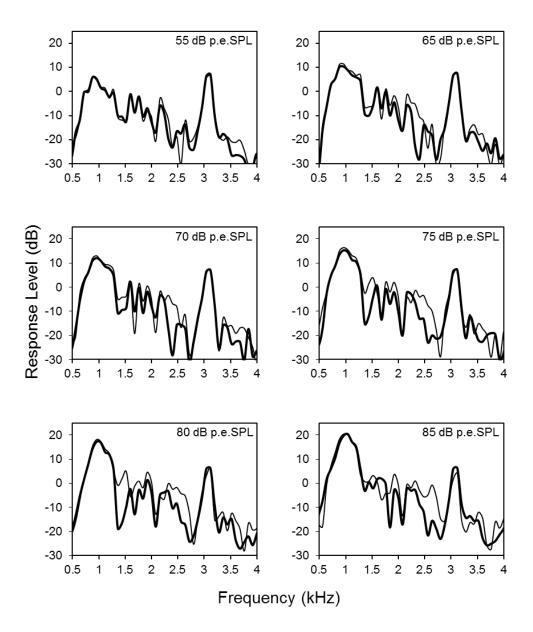


Figure 6. Spectra for complex (bold line) and composite (fine line) for linear presentation conditions for another representative subject. Again, close correspondence between spectra and suppression along the high-frequency slopes of the peaks at 1 kHz and 2 kHz can be observed.

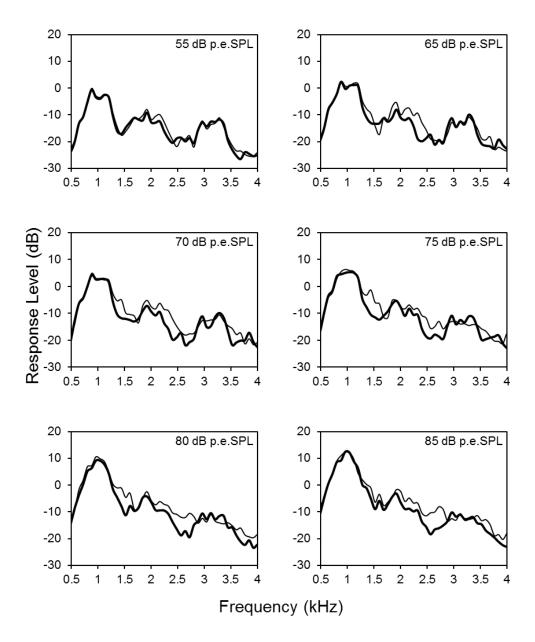


Figure 7. Mean spectra for complex (bold line) and composite (fine line) for linear presentation conditions across all ears. As with individual ears, it can be seen that there is a tendency for the suppression evident along the high-frequency portions of the peaks at 1 and 2 kHz in the complex spectra to increase with stimulus level.

Figure 8 shows the mean composite and complex spectra across all ears for both stimulus presentation paradigms, at a stimulus level of 75 dB p.e. SPL (the highest level used for the nonlinear paradigm). As expected, the levels of both the composite and complex spectra obtained using the nonlinear presentation paradigm were lower than those from the linear

presentation paradigm. However, as apparent in figure 8, the data obtained under both paradigms reveal similar levels of suppression. This was also the case for the other spectra obtained at the other two stimulus levels at which the linear and nonlinear paradigm were both used in the present study (65 and 70 dB p.e. SPL). Figure 9 compares the mean suppression occurring in bands B4, B5, B7, B8 and B9, for stimuli presented using the linear and nonlinear paradigm at 75 dB p.e. SPL. In general, the amount of suppression within each band is very similar for the two paradigms, with the exception of B5, which shows approximately 3 dB greater suppression for the linear than the nonlinear. However, this was the only instance across all five bands and three stimulus levels where there was a significant difference between the suppression obtained in the two paradigms. A repeated measures ANOVA including all five bands and three stimulus levels confirmed that presentation paradigm had no significant influence (p > 0.05) on mean suppression.

Figure 7 indicates a tendency for the suppression evident along the high-frequency portions of the peaks at 1 and 2 kHz in the complex spectra to increase with stimulus level. Figure 10 further explores this relationship by plotting the mean suppression in dB within the 240-Hz bands centred at 1.56 kHz (B5) and 2.52 kHz (B9) versus stimulus level.² A near-monotonic increase in suppression is observed up to a stimulus level of 75 dB p.e. SPL in both cases, with maximum suppression values of approximately 6.8 and 5.3 dB at 1.56 kHz and 2.52 kHz respectively. For a further increase in stimulus level to 85 dB p.e. SPL, the amount of suppression appears to drop dramatically for the 1.56 kHz band, and stay relatively constant for the 2.52 kHz band. A repeated measures ANOVA confirmed level as a significant factor (p < 0.005) on suppression.

² These frequency bands represented the ones demonstrating greatest suppression.

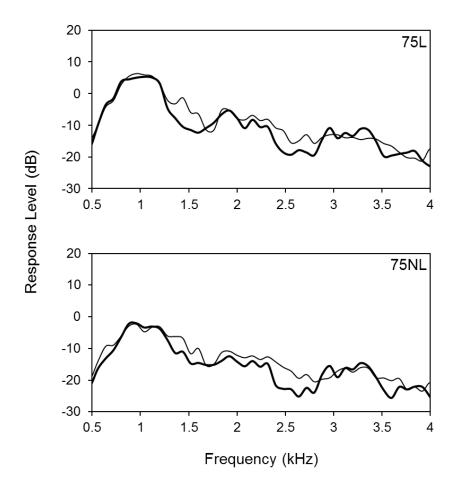


Figure 8. Mean spectra across all ears for complex (bold line) and composite (fine line) for linear (L) and nonlinear (NL) presentations at 75 dB p.e. SPL, the highest level used for the nonlinear paradigm. The levels of both the composite and complex spectra obtained using the nonlinear presentation paradigm were lower than those from the linear presentation paradigm. However, similar suppression can be observed for both presentation paradigms.

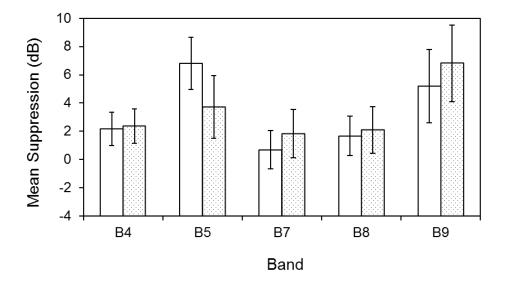


Figure 9. Mean suppression occurring in bands B4, B5, B7, B8 and B9 (corresponding to the high-frequency slopes of the peaks at 1 kHz and 2 kHz) for stimuli presented using the linear and nonlinear (shaded columns) paradigm at 75 dB p.e. SPL. Error bars represent 95% confidence intervals. Suppression is similar for both paradigms, except in band B5. However, this was the only instance where suppression was significantly different between paradigms, for all three stimulus levels where the linear and nonlinear paradigms were used.

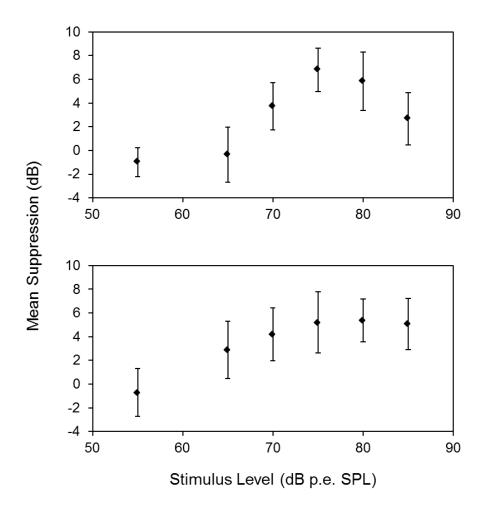


Figure 10. Dependence of mean suppression on stimulus level within 240-Hz bands of centred at 1.56 kHz and 2.52 kHz. Error bars represent 95% confidence intervals. All stimuli represented were presented linearly. A near monotonic increase in mean suppression is observed up to a stimulus level of 75 dB p.e SPL for the bands centred at 1.56 kHz and 2.52 kHz, with a mean suppression value of approximately 6.8 dB and 5.3 dB respectively. For a further increase in stimulus level to 85 dB p.e SPL, the amount of mean suppression appears to drop dramatically for the 1.56 kHz band and stay relatively constant for the 2.52 kHz band.

Discussion

Many previous studies have demonstrated results that are broadly consistent with the principle of local, independent TEOAE generator channels (e.g. Kemp, 1978; Probst *et al*, 1986; Xu *et al*, 1994; Prieve *et al*, 1996; Tavartkiladze *et al*, 1997; Ueda, 1999). However, data from two particular studies (Xu *et al*, 1994; Yoshikawa *et al*, 2000) have suggested an element of interaction between such channels, observed as a reduction in the response at one frequency due to simultaneous presentation of additional slightly higher frequency tone bursts. This "suppression" occurred under certain conditions, namely at high stimulation levels presented using the nonlinear paradigm. Although raised stimulus levels were postulated as the cause of suppression, it was also possible that the observed suppression occurred as a result of the presentation paradigm or a combination of stimulus level and presentation paradigm.

The results of the present study confirm the observation of suppression of the type reported by Xu et al (1994) and Yoshikawa et al (2000). In keeping with these two previous studies, significant suppression is found across the high-frequency portion of the 1 and 2 kHz peaks in the complex spectra, but not in the 3 kHz peak. However, the present results also demonstrate that although there is a clear reduction in both complex and composite responses due to the use of the nonlinear presentation paradigm, the actual difference between complex and composite responses (i.e., suppression) is the same in both presentation paradigms. This confirms that the degree of suppression is indeed a function of stimulus level, as suggested by Xu et al (1994) and Yoshikawa et al (2000), and is not materially influenced by the use of a nonlinear rather than a linear presentation paradigm (at least for subjects with the degree of TEOAE input-output nonlinearity in our sample).

The secondary aim of our study was to characterise in greater detail the effect of stimulus level on this type of TEOAE suppression. Previous studies (Xu *et al*, 1994; Yoshikawa *et al*, 2000) have suggested that suppression increases with stimulus level. However, data presented from those studies suggested an abrupt onset of suppression at the higher stimulus levels (above 70 dB p.e. SPL), with no significant suppression at lower levels. In contrast, the results of the present study suggest a systematic increase of suppression with increase of stimulus level. This near-monotonic relationship is observed for suppression occurring along the high frequency portions of the spectral peaks at both 1 and 2 kHz up to a level of 75 dB p.e. SPL. The progressive increase in suppression with stimulus level may suggest that the suppression mechanism is intimately linked to TEOAE input-output nonlinearity.

Increase in stimulus level above 75 dB p.e. SPL resulted in a breakdown in the monotonic increase in suppression – suppression dropped for the high frequency portion of the 1 kHz peak and remained relatively constant for the high frequency portion of the 2 kHz peak. It is most likely that this apparent reduction or levelling out in the suppression in fact reflects a substantial contamination of the TEOAE by extended stimulus ringing at these high stimulus levels. As such stimulus ringing is essentially linear, it would not exhibit any suppression, i.e. there would be little difference between the stimulus ringing due to the complex stimulus and the summation of that due to the individual stimuli.

The present study has additionally shown a greater extent of suppression of the 2 kHz response component than was evident in the study by Xu *et al* (1994). Xu *et al* (1994) report significant suppression of the high frequency portion of the 2 kHz peak at the highest stimulus level (75 dB p.e. SPL) only. In contrast, data from the present study demonstrated significant levels of suppression, predominantly at the higher frequency portion of the 2 kHz peak, for all

levels. This apparent difference in suppression of the spectral peak at 2 kHz is likely to be accounted for by the use of time windows of differing length when analysing responses. The present study used an analysis window of 8 - 20.44 ms whereas Xu *et al* utilised an earlier analysis window of 5.5 - 20.5 ms. It is possible that their earlier window may have included a significant proportion of stimulus energy, which would not have demonstrated any suppression.

The mechanism of suppression observed in this and previous similar studies is not clearly established. Xu *et al* (1994) appear to leave open the possibility that basal areas of the cochlea, well remote from the region of excitation due to a particular tone burst, may have been involved in the suppression observed in their data. The involvement of remote basal regions of the cochlea in TEOAE generation has been suggested by other authors (Sutton, 1985; Avan *et al*, 1995; Avan *et al*, 1997; Withnell and Yates, 1998).

However, an interesting question is whether the data, both of Xu *et al* (1994) and the present study, necessarily implicate the involvement of such basal regions, or whether they simply indicate the local, relatively restricted, spread of excitation within the cochlea due to a tone burst of a particular frequency. Nonlinear interactions as a result of such spread of excitation due to, say, the 1 kHz and 2 kHz tone bursts, could result in the suppression of the high-frequency side of the 1 kHz response peak as reported in the present study. Such suppression would be analogous to two-tone suppression (2TS) as demonstrated in direct measures of cochlear mechanics (e.g. Cooper, 1996). The finding, both in our study and in previous similar work, of suppression predominantly on the high-frequency slopes of the 1 kHz and 2 kHz response peaks, but not on the 3 kHz peak, is also consistent with a mechanism common to that of 2TS, as high-frequency suppressors are known to be more effective than low-

frequency suppressors in 2TS (Cooper, 1996). Preferential suppression of the high-frequency side of the lower-frequency tone burst (rather than the low-frequency side of the higher-frequency tone burst) within such a mechanism is also consistent with most models of the role of the active process, which indicate it is restricted to the basal region, i.e. the high-frequency side, of a particular excitation pattern (e.g. Neely and Kim, 1986; Kolston, 2000). Further, Konrad-Martin and Keefe (2003, 2005) have reported a spectral asymmetry within the TEOAE evoked by a simple-tone burst, which they attribute to "within-band" suppression of the low-frequency component of such a TEOAE by the (slightly) higher frequency components, again directly relating this to 2TS. Finally, this interpretation of our findings is also consistent with the suppression of stimulus frequency otoacoustic emissions reported by Brass and Kemp (1993), who found that, for equi-level suppressor and stimulus tones, a suppressor higher in frequency than the stimulus was more effective than one that was lower in frequency.

Yates and Withnell (1999) have argued that the stimulus frequencies used by Xu et al (1994) (and subsequently in this study) would generate travelling waves with little possibility for interaction. However, the bulk of relevant physiological data in the literature are derived from the basal turn in small laboratory mammals. In contrast, Cooper and Rhode (1996) report 2TS data from the apical turn of the chinchilla, showing far broader "tuning" of the phenomenon than in the basal turn (e.g. suppression of a 600 Hz response by a suppressor almost an octave higher). We would argue that this finding, combined with possible species differences, would allow the possibility of interaction between travelling waves generated by the frequencies used in this study. Further, Yoshikawa et al (2000) systematically varied the frequency separation between the components of their complex stimulus, and found maximum TEOAE suppression when the constituent tone bursts of the complex stimuli were

closest together (0.5 kHz). This again supports the notion of suppression being due to overlap between local excitation patterns, with increasing overlap as the frequency separation between the stimulus components is reduced.

We would therefore argue that the data of the present study, as well as Xu et al (1994) and Yoshikawa et al (2000) are suggestive of relatively local interactions in the generation of TEOAE component responses, rather than of widespread "remote" interactions. This in turn may strengthen the notion that TEOAE component responses are substantially locally generated, rather than generated over a wide region of the basilar membrane, as has been argued by Sutton (1985); Avan et al (1995); Avan et al (1997) and Withnell and Yates (1998) and Carvalho et al (2003).

The implication of local generation of TEOAE frequency components, is also important for the possible clinical application of TEOAEs as a tool for frequency-specific objective assessment of hearing loss.

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